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POPULATION STUDIES OF EUROPEAN SPARROWS IN NORTH AMERICA

By

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The house sparrow *(Passer domesticus)* and the European tree sparrow *(P. montanus)* (hereafter identified as the tree sparrow) occur sympatrically over much of Eurasia. The two species are similar morphologically, and also have very similar ecologies, both being primarily granivorous and commensals of man. Both species were also successfully introduced into North America during the nineteenth century.

The house sparrow was first introduced into the eastern United States at New York City in 1853 (Barrows 1889). Subsequently, repeated introductions of sparrows from England and Germany were made at various places in the eastern United States until 1881. The species rapidly expanded its range westward with the intentional and unintentional aid of man. By 1893 it had established a transcontinental range in North America (Wing 1943) that today extends from Guatemala (Thurber 1972) north through the southern tier of Canadian provinces.

Twenty individuals of the tree sparrow were imported from Germany and released in Saint Louis, Missouri on 25 April 1870 (Widmann 1889). During the 1870's the species multiplied rapidly, and came to occupy much of the Saint Louis metropolitan area. However, with the arrival of the house sparrow to the Saint Louis area in the late 1870's in the course of its westward expansion, the tree sparrow disappeared from the urban area it had occupied pre-

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viously (Widmann 1889). Since that time it has persisted primarily in rural areas, and gradually has extended its range northward. It currently occupies a range of approximately 22,015 km^2 (8,500 mi^2) (Barlow 1973), extending about 160 km north from Saint Louis.

The purposes of this study were twofold: (1) to study the ecology of the tree sparrow in North America, and (2) to attempt to answer some of the questions raised by its very restricted range in North America. These questions can be stated in the following general form: (1) Are there competitive interactions between populations of the house sparrow and the tree sparrow in North America? (2) If so, what interactions may be involved in limiting the distribution of the tree sparrow? (3) If not, how are the two species partitioning their resource environment? To accomplish these objectives, I conducted concurrent population studies of the house sparrow and the tree sparrow and examined resource utilization patterns of the two species in areas of potential competition.

Several pieces of evidence suggest that the house sparrow might be involved in the restriction of the tree sparrow in North America. The similar ecologies of the two suggest the possibility of competitive interaction. Historical evidence also suggests the possible restrictive role of the house sparrow. In addition to the displacement of the tree sparrow from the Saint Louis urban area witnessed by Widmann, other similar events have been observed. On several of the smaller islands in the British Isles the tree sparrow was formerly a common resident, but disappeared after the house sparrow colonized the islands (Summers-Smith 1963). The wide distribution of the tree sparrow in Eurasia suggests that the species would not be limited on the North American continent by climate or other abiotic features of the environment. In addition, man has altered the environment of North America, particularly by clearance for agriculture, in much the same way as he did in Eurasia, and it is in this altered biotic community that the tree sparrow resides.

Population studies of both the house sparrow and the tree sparrow have been reported from Europe (Summers-Smith 1963, Pinowski 1968). Several studies on the breeding biology of the house sparrow in North America have been published (Weaver 1943, Will 1969, North 1972, Mitchell *et al.* 1973). Concurrent studies of the breeding biologies of both species have been conducted in England (Seel 1968a, b; 1969, 1970) and Poland (Mackowiez *et al.* 1970, Pinowski and Wieloch 1972). No study of the tree sparrow in North America has been reported, however (Barlow 1967).

Three areas of potential interaction between populations of house sparrows and tree sparrows in the utilization of resources were studied in an attempt to answer the questions posed above. Two of these areas involved potential competition for food, one during the winter, and the second during the breeding season. The highest rate of adult mortality in tree sparrows in Poland is from January to March (Pinowski 1968). Food shortage or unavailability is a possible reason for the high rate of mortality. The highest rate of adult mortality in the house sparrow in England, on the other hand, is during the breeding season from May to August (Summers-Smith 1963). The high energy demands of reproduction may contribute to the high mortality rate at this season. Beimborn (1967), however, found that the highest mortality rate of the house sparrow in North America was in the winter, from October to March. The possibility of competition for food during these two seasons between the two species was therefore examined in this study.

The availability and utilization of nest sites was the third area of potential interaction examined in this study. Observations by Widmann (1889) suggest that house sparrows displace tree sparrows from favored nest sites. It has been shown that nest sites are frequently a limiting factor for populations of hole-nesting birds (von Haartman 1971).

METHODS AND MATERIALS

Study Area.—A study area consisting of three sites was selected near Portage des Sioux, Saint Charles County, Missouri (38° 55′ N, 90° 22′ W). The study area is located on the floodplain between the Mississippi and Missouri Rivers near their confluence. Most of the land in the immediate vicinity is cultivated, the principal crops being corn, soybeans and winter wheat.

Site A is an abandoned farmstead 1.6 km north of Missouri highway 94 on Rees Road. The site consists of two buildings, a barn and wire-mesh enclosed granary, both of which are used only for grain storage. The only tree at the site is a large red mulberry *(Morus rubra)*. Observations were made at this site from mid-June 1968 through September 1973.

Site B is an occupied farmstead 1.7 km east of site A, and is located at the intersection of Weber Lake Road and an unnamed dirt road. The site contains thirteen buildings (including two steel grain bins) and many large trees, principally silver maples *(Acer saccharinum)* and Siberian elms *(Ulmus pumila)*, but also including some American elms *(Ulmus americana)* (some dead), red mulberries and black locusts *(Robinia Pseudo-Acacia)*. During most of the study horses and pigs were kept at the site, and a few cattle were kept there from 1971 to 1973. Observations at this site were begun in mid-June 1968 and continued through September 1973.

Site C is located at Racoon Ranch, a wildlife preserve and managed duck-hunting area owned by the Hager Hinge Company of Saint Louis. The site actually used in this study was the area around the support buildings of the ranch (resident caretaker's house, two clubhouses, machine shop and two garages), and is 1.9 km north of site A. North of the support buildings is a woodland-edge habitat in which pin oaks *(Quercus palustris)* and black walnuts *(Juglans nigra)* predominate, and along with a few silver maples and American elms result in an almost completely closed canopy. A parkland area east of the support buildings contains scattered black walnuts. Nest-boxes were placed in these two areas in March 1970. Observations at site C began in March 1970 and continued through August 1972.

Population Study.—Concurrent population studies of the house sparrow and tree sparrow were initiated in the summer of 1968. Beginning in mid-June data were collected on the breeding efforts of house sparrows at two sites (A and B) in the study area. Visits to nest sites were made at 3 or 4 day intervals. Data collected for each nesting effort were: date of initiation of the clutch, clutch size, date of hatching, number of eggs hatching and number of young fledging successfully. Each surviving young sparrow was banded prior to fledging with a USFWS band (permit number 9323).

During the winter of 1968-1969 nest-boxes were constructed and placed on trees at various locations at site B. Each was constructed with a hinged lid so that the contents could be readily examined. Most were made with an entrance hole with a diameter of 29 mm, which allows the tree sparrow to enter, but excludes the somewhat larger house sparrow (see below). The regular routine of visits to nest sites established in 1968 was continued for all nest sites and nest-boxes during the 1969, 1970, 1971, 1972, and 1973 breeding seasons. In addition to the data mentioned above, beginning in 1970 and continuing into the middle of the 1972 breeding season, nestlings at site B were weighed to the nearest 0.1 g on a triple-beam balance at the time of banding. Thirty nest-boxes were placed on trees at site C in March 1970, each constructed with an entrance diameter of 29 mm. Regular visits to nest sites and nest-boxes at site C began in 1970, and continued through 1972.

Beginning in late summer 1969, Japanese mist nets were employed to capture adult sparrows. Adult sparrows were weighed and banded. Recapture data on birds banded as nestlings and adults were used to estimate population sizes and mortality rates.

Resource Utilization.—Nestling Food: The pipe-cleaner method described by Orians (1966) was employed to sample the food provided to nestling house sparrows and nestling tree sparrows. The food items obtained from all the nestlings in one brood in an hour constituted a sample. Matched samples were obtained by simultaneously sampling broods of both species containing nestlings of the same age.

Samples were refrigerated at 4° C until the contents could be identified. Adult insects were keyed out at least to family, while larval insects were keyed out to order. All identifications were performed using a binocular microscope. The length of each item was measured using a metric rule, and the weight of each item was obtained on a Mettler Balance (to 0.1 mg) after air drying for 24 hours.

Winter Food: A feeding platform was erected at site B to study intraspecific and interspecific interactions at a common feeding location. The platform was rectangular, measuring 0.6 by 0.9 m. Johnston (1969) has reported on intraspecific aggressive behavior of house sparrows at a similar winter feeding station. The platform was intentionally constructed so that the food was not a point resource, i.e. it would be possible for more than one individual to feed simultaneously. This was done so that the station would more closely resemble the natural winter food resources of these social feeders. Observational techniques were used to study interactions between house sparrows and tree sparrows. The fundamental question was whether interspecific aggressive behavior exceeded intraspecific aggressive behavior in frequency or intensity, and if it resulted in the exclusion of one species from the feeding station.

Nest Sites: In 1971 there were 36 nest-boxes at site B, 27 with entrance holes of 29 mm diameter. Most of these nest-boxes (29 mm) had been used exclusively by tree sparrows. During September 1971, the entrance holes of 21 of the 27 nest-boxes were enlarged to a diameter of 31 mm. Utilization of these nest-boxes during the 1972 and 1973 breeding seasons was observed to ascertain whether tree sparrows were excluded from many of the nest-boxes previously used by them.

RESULTS AND DISCUSSION

Population Study

Fecundity: Duration of the Breeding Season.—The date of initiation of a clutch is a convenient parameter for the analysis of temporal patterns of breeding. Moreau (1950) defined the breeding season of a species in an area as the period from the initiation of the first clutch to the initiation of the last clutch. Table 1 presents data on the duration of the breeding seasons of the two sparrows near Portage des Sioux (Table 1 and all other tables are found in the Appendix following the Literature Cited).

The mean dates for the initiation of the first clutch of the season were 30 March for the house sparrow and 20 April for the tree sparrow (18 April if the small 1969 sample is ignored). A similar difference in the initiation of the breeding seasons of the two species has also been reported in areas of sympatry in England and Poland (Seel 1968a, Mackowicz *et al.* 1970). This difference is possibly of considerable significance in interactions between the two species for nest sites (Summers-Smith 1963), and will be discussed further below.

The mean date for the initiation of the last clutch of the season for the house sparrow was 10 August and the mean duration of the breeding season for the species near Portage des Sioux was 132 days. The mean date for the initiation of the last clutch of the season for the tree sparrow was 7 August (10 August if 1969 is ignored). The mean duration of the breeding season of the tree sparrow was therefore 109 days (113 days if 1969 is ignored). The difference between the mean duration of the breeding season of the house sparrow (1969-1973) and that of the tree sparrow (1970-1973) is statistically significant ($t=2.657$, $P<0.05$).

Fecundity: Temporal Distribution of Breeding.—The temporal distributions of house sparrow clutches was fairly consistent in the five seasons from 1969 to 1973. In three of the five seasons the highest percentage of clutches fell in the second 10-day period of April, while in the other two seasons the highest percentage of clutches was during the third 10-day period of April. Lesser peaks of clutch initiation usually occurred in the third 10-day periods of May, June and July. Renesting attempts following the failure of clutches diluted the synchrony of the breeding pattern, but did not conceal it altogether. The four peaks correspond to the peak laying periods of four clutches, although many of the clutches in the last peak represented renesting efforts.

The annual pattern of distribution was even more consistent for the tree sparrow than for the house sparrow. Four peaks occurred in 1970 and 1972, while there were three peaks in 1969, 1971 and 1973 (the small sample size in 1969 makes it appear that there were four peaks). The first peak was in the third 10-day period of April in all five seasons, with subsequent peaks usually occurring in the third 10-day period of May and the first 10-day period of July. The fourth peaks in 1970 and 1972 represented fourth clutches in those years, and fell in the first 10-day period of August.

Fecundity: Incubation Period.—True incubation is apparently performed only by the female in both the house sparrow and the tree sparrow because in neither species does the male develop a brood patch (Summers-Smith 1963; pers. obs.). The female of both species develops a prominent brood patch, and this difference was the principal means of identifying the sex of adult tree sparrows during the course of this study. Males of both species were frequently captured on the nest during the incubation period, however, and they therefore apparently cover the eggs during periods when the female is foraging. This coverage may well perform the dual function of protecting the eggs from predation and retarding the cooling rate of the eggs during the absence of the female.

The incubation period of birds is commonly defined as the length of time from the laying of the last egg in a clutch to the hatching of that egg (Thomson 1964). Determination of this period requires daily observations of the clutch from the onset of egg laying until hatching, as well as marking of individual eggs. Because this observational routine is not always practicable, other operational definitions of incubation period have been used. Such a definition, which is more suitable for the observational routine of this study, is the number of days from the laying of the first egg in a clutch until the hatching of at least one egg (North 1972). The determination of this period, the clutch initiation-hatching interval, in this study depended largely on the somewhat fortuitous event of an observation day coinciding with some evidence that that day was the hatching day for the first egg or eggs in the clutch.

Data on the clutch initiation-hatching interval for the two species are recorded in Table 2. This interval varied from 11 to 17 days for the house sparrow, with a mean of 14.1 days. For the tree sparrow the interval varied from 13 to 18 days, with a mean of 14.9 days. The difference between the two species is highly significant ($t=3.092$, $P<0.01$).

Clutches initiated early in the season required longer to hatch than later clutches (see Table 2). The mean interval for house sparrow clutches initiated prior to 11 May was 14.7 days, and the mean for clutches initiated from 11 May until the end of the breeding season was 13.9 days. The difference is highly significant ($t=3.713$, $P<0.001$). In the tree sparrow the mean interval for clutches initiated prior to 21 May was 16.0 days, and for clutches initiated from 21 May until the end of the breeding season, 14.3 days. The difference is also highly significant ($t=4.183$, $P<0.001$). This difference is possibly the result of retarded embryonic development due to more chilling of the eggs during the late spring than during the summer. Novotný (1970) reported a gradual decrease in the incubation period from the first to the third clutches of the house sparrow at Slezské Rudoltice, Czechoslovakia.

Large clutches required longer periods to hatch than small clutches (see Table 2). House sparrow clutches of 2, 3 and 4 eggs had a mean clutch initiation-hatching interval of 13.0 days while clutches of 5 and 6 eggs had a mean interval of 14.3 days ($t=3.417$, $P<0.01$). Tree sparrow clutches of 4 and 5 eggs had a mean interval of 14.4 days while clutches of 6 and 7 eggs had a mean interval of 16.0 days ($t=3.509$, $P<0.01$). This suggests that incubation begins later in large clutches than in small clutches.

Seel (1968b) found the mean incubation period *(sensu stricto)* for the two species to be identical at Oxford (house sparrow, 11.45 days and tree sparrow, 11.49 days). The difference in the mean clutch initiation-hatching interval between the two species found in the present study may therefore be due to the fact that the tree sparrow has a larger mean clutch size (cf. Table 6). Table 3 therefore shows the clutch initiation-hatching intervals for the two species for clutches of 5 eggs. The mean interval is 14.2 days for the house sparrow and 14.5 days for the tree sparrow, and the difference is not statistically significant ($t=1.465$, $P>0.10$). Subtracting the incubation period *(sensu stricto)* found by Seel for the two species from the mean clutch initiation-hatching interval for clutches of 5 eggs leaves approximately 3 days, and suggests that both species begin incubation on the antipenultimate day of egg laying. Weaver (1943) reported that incubation usually began with the third egg for the house sparrow at Ithaca, New York (modal clutch size 5).

Fecundity: Nestling Period.—The nestling periods of the two sparrows were determined from observations on the date of fledging, which was in turn determined by observing young leaving the nest. Disturbance by the investigator was frequently the stimulus inducing young sparrows to leave the nest so that the nestling periods determined on the basis of these observations are minimum periods. Only cases in which the departing young were capable of sustained flight were used in order to minimize the impact of this observer-created bias.

The nestling period was obtained by subtracting the mean incubation interval of each species from the mean clutch initiation-fledging interval (Table 4). The nestling period of the house sparrow was 14.8 days, and the nestling period of the tree sparrow was 14.0 days.

Fecundity: Interval Between Successive Clutches.—Approximately one week elapses between the fledging of the young in one clutch and the initiation of the next clutch at that site for both the house sparrow and the tree sparrow. This interval was determined by subtracting the clutch initiation-fledging interval from the mean interval between the initiation of successive clutches at the same site (when the first clutch resulted in the successful fledging of at least one young). The number of days between the initiation of successive clutches in the house sparrow varied from 28 to 49 days (sites at which the elapsed interval between successive clutches exceeded 50 days were considered to be the result of some abnormal occurrence, and therefore were ignored). The mean interval was 36.8 days ($n=170$, $s\bar{x}=0.25$). The interval between successive clutches of the tree sparrow varied from 28 to 49 days, with a mean of 36.4 days ($n=85$, $s\bar{x}=0.38$). The difference between the two species is not significant ($t=0.898$, $P>0.20$).

Subtracting the mean clutch initiation-fledging interval of each species from the mean interval between successive clutches yields 7.9 and 7.5 days for the house sparrow and the tree sparrow, respectively. Thus an average of 7 to 8 days elapses between the fledging of one clutch and the initiation of the next clutch.

Fecundity: Number of Clutches per Pair-Season.—The house sparrow was normally double- or triple-brooded near Portage des Sioux, and only rarely quadruple-brooded. The tree sparrow was normally triple-brooded, less commonly double-brooded, and only rarely quadruple-brooded. Critical evidence for the existence of fourth clutches in both species was obtained during 1970. In that year, females of each species were captured at the nest during incubation of the first clutch, and again at the same nest site on fourth clutches after each of the preceding clutches had successfully fledged young.

Table 5 summarizes data on the mean number of clutches per nest site-season for the years 1969-1973 for both species. The mean for the five years for the house sparrow was 2.40 clutches per nest site, but varied widely from 2.06 in 1970 to 3.23 in 1973.

The mean number of clutches per nest site-season for the tree sparrow was 2.61. Variation between seasons was greater for the tree sparrow than the house sparrow, ranging fom 1.83 in 1969 to 3.11 in 1972.

The difference between the mean number of clutches per nest site-season of the house sparrow and the tree sparrow is not significant ($t=1.344$, $P>0.10$).

Fecundity: Clutch Size.—Data on the clutch sizes of the two species are presented in Table 6. The clutch size of the house sparrow varied from 2 to 8 with 5 being the mode. The mean clutch size near Portage des Sioux, based on the five complete seasons of observation, was 4.64. The clutch size of the tree sparrow varied from 2 to 7 with 5 again being the mode. The mean clutch size was 4.99 for the five seasons. The difference between the mean clutch size of the house sparrow and that of the tree sparrow is highly significant ($t=4.984$, $P<0.001$).

In a recent review of the ecological aspects of avian reproduction, Cody (1971) listed nine factors known to influence clutch size: age of parent, the time of breeding or the order of the clutch within the season, food supply, population density, latitude, longitude, elevation, habitat and nest site. Latitude, longitude and altitude refer to differences between populations, and except for a latitudinal comparison of clutch size in the house sparrow from various localities in the continental United States, there will be no discussion of these factors. Habitat differences may refer to differences between distinct populations occupying different habitats, or to changes within a population occupying a range of habitat types. Age of parent, expressed at the population level as an altered age structure, food supply and population density generally constitute between season variables affecting clutch size within a population. As Cody pointed out, these variables are not necessarily independent of each other. The time of breeding or the order of the clutch within the breeding season refers to seasonal changes in clutch size within a population. The nest site factor as discussed by Cody refers to interspecific variation in clutch size with a gradient in nest site types, with mean clutch size of mid-European passerines increasing with the gradient from open nests to domed nests to nests in holes and other protected sites (Cody 1971).

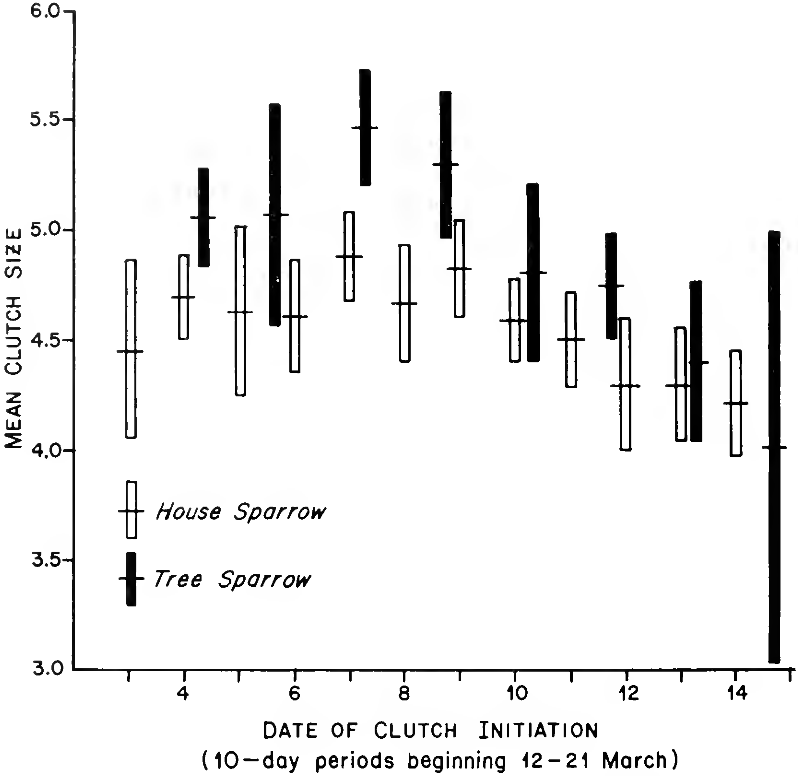

FIG. 1—Seasonal change in clutch sizes of the house sparrow and tree sparrow near Portage des Sioux, Missouri (mean ± 2 S. E.).

The changes in clutch size of both sparrows during the course of the breeding season are depicted in Fig. 1. The clutch size of the house sparrow was relatively constant from mid-April through the first part of July, fluctuating only between approximately 4.6 and 4.9. Earlier clutches averaged only about 4.4, however, and in late July and August, clutch size decreased markedly, to about 4.2 for the period 30 July-18 August. Clutch size in the tree sparrow was highest during the middle of the breeding season (5.3 to 5.5 for clutches initiated during late May and early June), and was smaller at both the beginning and end of the breeding season (about 5.0

for April and early May, and 4.8 down to 4.0 for late June, July and August). Seel (1968b) noted similar patterns of seasonal variation in clutch size in the two species at Oxford. This general pattern, particularly the decline in clutch size during the latter part of the breeding season, has been reported for many other bird species (see Klomp, 1970).

The clutch size of the house sparrow was relatively constant between different years of the study, and there are no significant differences between years. The clutch size of the tree sparrow, on the other hand, showed marked differences between different years. The decrease in clutch size during the years 1971-1973 coincided with an increased number of breeding pairs at study site B during those years. Most tree sparrows breeding on the study area utilized nest-boxes as nest sites. Activity was observed around natural cavities in tree limbs in 1969, 1971, and 1973, but only in 1973 was it certain that such a site was used for nesting. Therefore, the number of pairs utilizing nest-boxes simultaneously was a good estimate of breeding density for the species. The maximum numbers of tree sparrow pairs using nest-boxes simultaneously were: 1969, 4 pairs; 1970, 9 pairs; 1971, 22 pairs; 1972 and 1973, 17 pairs. It is readily apparent that the number of pairs increased dramatically at study site B during the first three years of the study, more than doubling each year. The mean clutch sizes of the three more populous years, 1971-1973, were much lower than the mean clutch sizes of the lower density years, 1969 and 1970. The combined mean clutch size for 1969 and 1970 was 5.38, and the combined mean for 1971-1973 was 4.91, and the difference is highly significant ($t=2.882$, $P<0.01$). The product-moment correlation coefficient (r) between the number of pairs at study site B and the mean annual clutch size is very high, $r=-0.9369$ ($P<0.01$). Mean clutch size is plotted against number of breeding pairs in Fig. 2. The regression equation is:

$$Y=5.55-0.033X.$$

An inverse relationship between clutch size and density has been reported for several other species of birds (see Klomp, 1970; Cody, 1971). The decline in clutch size may also have been related in part to an altered age structure in the expanding population (see below).

Fig. 2 also depicts the change in mean clutch size of the house sparrow at site B with the increasing breeding density of tree sparrows. Mean clutch sizes of the house sparrow at study site B for the five years were: 1969–4.62; 1970–4.63; 1971–4.82; 1972–4.71; and 1973–4.70. Although the differences are not great, the product-moment correlation coefficient between the number of tree sparrow breeding pairs and mean clutch size of the house sparrow at site B is very high, $r=0.9247$ ($P<0.01$). This observation is of interest

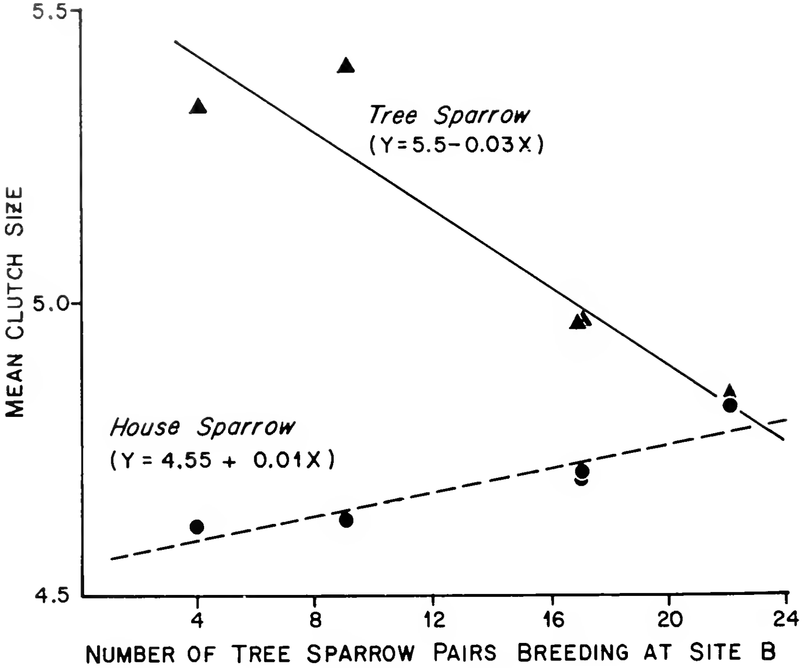

FIG. 2—Mean clutch sizes of the house sparrow and tree sparrow at Site B plotted against number of breeding pairs of the tree sparrow.

because it contradicts the expectation, on theoretical grounds, that reproductive commitment should decrease in the presence of increased competition (Cody, 1971). The mean clutch size of the house sparrow at McLeansboro, Illinois, which lies at the same latitude as Portage des Sioux and only 180 km away and where the house sparrow occurs in the absence of the tree sparrow, was also significantly lower than the mean clutch size near Portage des Sioux ($t=3.100$, $P<0.01$). This may reflect the importance of the intrinsic rate of increase (r) of a population in determining the outcome of competitive interactions, noted recently by Vandermeer (1975).

One possible explanation for the increased clutch size of the house sparrow in the years 1971-1973 would be an altered age structure in the breeding population. Nice (1937) for the song sparrow *(Melospiza melodia)*, Lack (1966) for the great tit *(Parus major)* and von Haartman (1967) for the pied flycatcher *(Ficedula hypoleuca)* recorded small clutch sizes for females in their first breeding season. Thus, mean clutch size for the population would tend to vary inversely with the proportion of first year birds. The breeding population of the house sparrow at site B remained relatively constant during the study (see below), so there is little reason to suggest that the variations in clutch size were due to changing age structure in the breeding population, although constancy of the size of the breeding population does not necessarily imply a stable age distribution. No independent survey of food availability during the five years was made, so the importance of this factor on clutch size is unknown. It may have played a role in the increased clutch sizes in the years 1971-1973, although this seems unlikely, with both species dependent on essentially the same food resources (see below).

The house sparrow utilized a variety of nest sites during the course of the study, ranging from nest-boxes and crevices in buildings to open sites in the forks of branches of trees. The mean clutch size of domed nests located in open sites in the branches of trees was 4.58 ($n=36$, $s\bar{x}=0.122$). The mean clutch size of nests located in all protected sites, such as nest-boxes, holes in trees and crevices in buildings, was 4.65 ($n=584$, $s\bar{x}=0.036$). There is apparently no intraspecific difference in clutch size correlated with nest site type in the house sparrow ($t=0.4835$, $P>0.60$).

In other North American studies the mean clutch size of the house sparrow varies from 4.23 at Plainview, Texas (Mitchell *et al.*, 1973) to 4.96 at Coldspring, Wisconsin (North, 1972). Will (1969) recorded a mean clutch size of 4.46 at McLeansboro, Illinois. All of these stations lie in mid-continental North America, and the positive relationship between clutch size and latitude is significant ($r=0.987$, $P<0.01$). The regression equation relating mean clutch size (Y) and latitude (X) in continental North America is:

$$Y=1.34+0.084X$$

A positive relationship between clutch size and latitude has been frequently observed in birds (see Cody, 1971). The existence of this relationship in North American populations of the house sparrow appears to provide further evidence of rapid adaptive change in this species (see Johnston and Selander, 1964; Hudson and Kimzey, 1966).

Clutch size has also been reported to increase in some species from west to east on continental land masses in Europe (Lack, 1968; Cody, 1971), and in North America (Johnston, 1954). The Coriolis force results in the prevailing winds being westerly at these temperate latitudes. The result would be that the western parts of these continental land masses would have their climates ameliorated somewhat by the influence of the maritime air masses pushed over them. The increases in clutch size from west to east and with increasing latitude would therefore parallel a decreasing temperature gradient in both cases. Bergmann's ecogeographic rule relates an increase in general body size with decreasing temperature, and this relationship has been observed in many birds (James, 1970), including the house sparrow in North America (Johnston and Selander, 1971). Therefore there may be a direct relationship intraspecifically between general body size and clutch size in birds, as there is in the lizard *Sceloporus undulatus* (Tinkle and Ballinger, 1972).

The clutch size of the tree sparrow has generally been found to be greater than that of the house sparrow in concurrent European studies. The clutch sizes at Oxford were house sparrow, 3.98 and tree sparrow, 5.05 (Seel, 1968b), at Dziekanów Lesny, Poland, house sparrow, 4.74 and tree sparrow, 4.91, and at Cracow, Poland, house sparrow, 4.51 and tree sparrow, 4.98 (computed from data in Mackowicz *et al.*, 1970 and Pinowski and Wieloch, 1972).

Fecundity: Hatching Success.—Data on hatching success in the two sparrows were collected on 653 clutches of the house sparrow and 216 clutches of the tree sparrow.

In the house sparrow 1,870 eggs hatched, 64.6% of the 2,894 eggs in undisturbed clutches. Table 7 summarizes the fate of the 1,024 eggs that failed to hatch. Some error is present in this statistic due to the observational routine of the study. Because nests were checked only every third or fourth day, a nestling could hatch from an egg on the day after an observation day and die in the next 24 to 48 hours, and if it was removed by the parents prior to the next visit by the observer, it would be recorded as an egg loss. Dead nestlings were regularly removed by the parents. Eggs failing to hatch frequently disappeared and were apparently removed by the parents as well, although sometimes they were not removed and remained in the nest with the nestlings. No correction can be made for this error, and therefore the hatching success figures are a minimum estimate. They are suitable, however, for comparisons between the two species.

In the tree sparrow 736 eggs hatched, 71.5% of the 1,030 eggs in undisturbed clutches. Table 8 summarizes the fate of the 294 eggs that failed to hatch.

Eggs that failed to hatch and which were not removed by the parents were opened and examined to determine the reason for the failure. Eggs were classified as infertile if they appeared to be fresh (bright yellow yolk) and showed no sign of embryonic development. Eggs in which embryonic development had occurred were classified into three categories according to the stage at which embryonic development had been arrested: (1) early embryonic death—evidence of development on the blastodisc but formed embryo not present; (2) mid-embryonic death—embryo formed and occupying about one-half of egg; and (3) late embryonic death—embryo fully developed and occupying most of all of the egg. Some eggs were addled or their contents were dried completely, probably due to a small break in the shell. Table 9 summarizes the results of the examinations of eggs which failed to hatch. The differences between the two species are not significant ($X^2=8.542$, $P>0.05$).

The difference in hatching success between the house sparrow and the tree sparrow is highly significant ($X^2=15.957$, $P<0.001$). The difference in hatching success was due both to the destruction of entire clutches and to the failure of eggs to hatch in successful clutches (cf., Tables 7, 8). Predation and weather (wind and rain) could affect different nest sites differentially. Nest-boxes were virtually immune from destruction by wind and rain, and also would exclude certain possible predators such as the blue jay *(Cyanocitta cristata)* and the common grackle *(Quiscalus quiscula).* They were, however, subject to predation by the black rat snake *(Elaphe obsoleta)*, a common predator from which many of the house sparrow nest sites located on buildings were immune. Tree sparrows utilized nest-boxes almost exclusively during this study, but house sparrows utilized a variety of nest sites in addition to nest-boxes. Many of these sites were obviously more subject to destruction by predation or weather than were nest-boxes. Therefore the hatching success of house sparrow clutches in nest-boxes was analyzed separately. The results are summarized in Table 10. In 236 clutches in nest-boxes, 68.8% of the 1,118 eggs hatched. This success rate is significantly higher than the 62.0% rate of hatching success in all other nest sites of the house sparrow ($X^2=13.843$, $P<0.001$). There is no significant difference between the hatching success of house sparrow clutches in nest-boxes and the hatching success of tree sparrow clutches ($X^2=1.819$, $P>0.10$).

In other concurrent studies of the two species, hatching success in the tree sparrow was found to be higher than that in the house sparrow. Seel (1968a,b) recorded hatching success rates of 76.1% and 82.9% for the house sparrow and the tree sparrow, respectively, at Oxford. In Poland, hatching success was 67.1% and 74.8%, respectively, at Dziekanów Lesny, but 79.0% and 79.2% at Cracow (computed from data in Mackowicz *et al.*, 1970; Pinowski and Wieloch, 1972).

Fecundity: Fledging Success.—Data on the fledging success of the two sparrows were collected on 506 broods of the house sparrow and 169 broods of the tree sparrow.

In the house sparrow 1,158 young fledged successfully, 62.8% of the 1,844 young in the undisturbed broods. Table 11 summarizes the fate of the young which died prior to fledging. In the tree sparrow, 513 young fledged, 72.4% of the 709 young in the undisturbed broods. Table 12 summarizes the fate of the young that died prior to fledging.

The difference in fledging success between the house sparrow and the tree sparrow is highly significant ($X^2=20.651$, $P<0.001$). The difference in fledging success appears to be in the failure of entire broods, this comprising 21.4% and 10.9% of all young hatched in the house sparrow and tree sparrow respectively. As in the case of hatching success, predation and weather could affect different nest sites differentially. The fledging success of house sparrow broods in nest-boxes was therefore analyzed separately. Data on the success of 181 broods in nest-boxes are presented in Table 13. The fledging success rate of 62.0% was actually lower than the 63.3% success rate at all other sites, although the difference is not significant ($X^2=0.288$, $P>0.50$). Fledging success of the tree sparrow is significantly higher than the fledging success of house sparrows in nest-boxes ($X^2=17.043$, $P<0.001$).

Seel (1970) also found significantly higher fledging success in the tree sparrow during his concurrent studies of the two species at Oxford. Fledging success there was 45.4% in the house sparrow and 58.5% in the tree sparrow. At two stations in Poland where concurrent studies of both species were conducted, fledging success of the tree sparrow was also greater than that in the house sparrow: Dziekanów Lesny, 70.5% for the house sparrow and 80.7% for the tree sparrow; Cracow, 66.8% and 85.8% respectively (computed from data in Mackowicz *et al.*, 1970; Pinowski and Wieloch, 1972).

Fecundity: Growth of Nestlings.—Growth curves of nestling house sparrows and tree sparrows are depicted in Fig 3. Although most of the nestlings were weighed only at the time when they were banded, a few individuals were weighed on the day of hatching to obtain an estimate of the hatching weight. Incubation periods varied with clutch size and season (as noted above) and hatching commonly required more than one day. The observational routine of the study precluded the precise determination of the date of hatching for most clutches. For the sake of uniformity, therefore, the day of weighing was calculated from the date of initiation of the clutch. Nestlings assigned to any one day were therefore not necessarily the same age. The general growth pattern of the nestlings appears to be clear, however (cf. Fig. 3). Nestlings of both species grow rapidly and reach maximum nestling weight by day 25 in both species. The mean weights of nestlings weighed on day 25 or later were: house sparrow, 23.1 g ($s\bar{x}=0.312$); tree sparrow, 17.4 g ($s\bar{x}=0.227$). Seel (1970) reported that the mean weights of nestling sparrows at Oxford on nestling day 13½ (approximately comparable to day 27 for the house sparrow and day 28 for the tree sparrow in this study) were 23.76 g for the house sparrow and 19.51 g for the tree sparrow.

Fecundity: Summary of Breeding Success.—The product of the hatching success proportion multiplied by the fledging success proportion is overall breeding success. It can be expressed as the

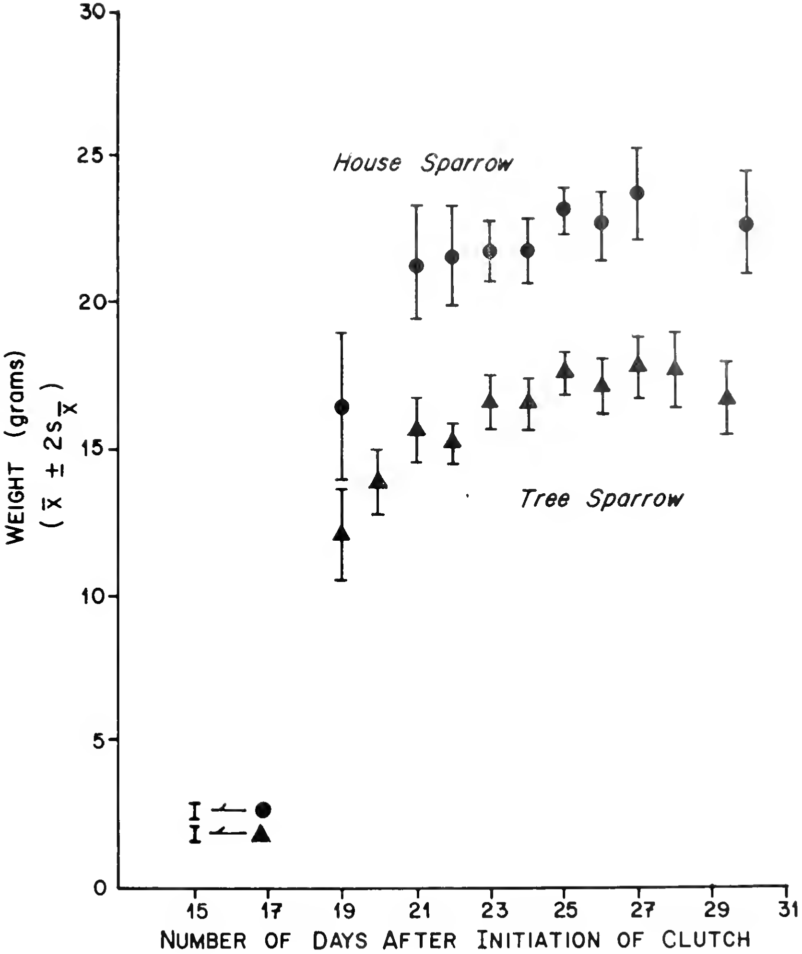

FIG. 3.—Rate of growth of nestling house sparrows and tree sparrows at site B.

percentage of eggs laid that result in fledged young. Tables 14 and 15 present a summary of the data on hatching success, fledging success and overall breeding success for the two species. A temporal breakdown of the data is also presented in the tables. The overall breeding success of the house sparrow was 40.6%, significantly lower than the 51.8% breeding success of the tree sparrow ($X^2=39.053$, $P<0.001$).

The time periods in the tables were chosen to coincide approximately with the peaks in the breeding seasons of the two species. The house sparrow usually has four peaks of clutch initiation (as mentioned above) which come at about 30-day intervals. Each of these peaks is placed in a different temporal category in Table 14. The tree sparrow shows three well-defined peaks of clutch initiation. The dates in Table 15 coincide approximately with the dates of these three peaks except that the dates have been changed slightly to coincide with the successive clutches of successful pairs, i.e., no third clutch was initiated prior to 25 June. Therefore, the three time periods coincide approximately with the three clutches usually laid by tree sparrow pairs.

Hatching success in the house sparrow varied from 58.3% to 69.4%. Hatching success in the third period (69.4%) is significantly higher than the hatching success in both the preceding period ($X^2=7.383$, $P<0.01$) and the succeeding period ($X^2=12.234$, $P<0.001$). Hatching success in the fourth period (58.3%) is significantly lower than that in the first period (65.2%: $X^2=5.339$, $P<0.05$). The reasons for these differences are unclear, particularly as there were no significant differences between the hatching success rates of the different time periods for the years prior to 1972. Hatching success in the tree sparrow varied from 70.1% to 73.4% with no significant differences between the three time periods.

Fledging success in the house sparrow varied from 52.9% to 89.0%, with the highest fledging rate being during the last period of the breeding season. Fledging success during the first period was significantly lower than during the other three periods ($X^2=16.065$, 17.893 and 74.362 respectively, $P<0.001$). The lower fledging success in the first period was due primarily to the fate of the first broods in 1973. General laying began earlier in 1973 than in the other years of study and an unseasonably cold period in early April, which began after many of the first clutches had hatched, resulted in an almost complete loss of the early broods. Prior to 1973 there was no significant difference between the fledging success of the first period and the succeeding two periods (Anderson, 1973). Fledging success in the last period is significantly higher than in the three earlier periods ($X^2=74.362$, 38.170 and 33.846 respectively, $P<0.001$). This pattern was consistent throughout the study. The same pattern was observed in the tree sparrow, where fledging success varied from 64.5% to 88.9%. The fledging success of 88.9% in the last period of the breeding season is significantly higher than in the preceding periods ($X^2=35.498$ and 28.727, $P<0.001$).

Will (1969) reported on the temporal patterns of hatching success and fledging success of the house sparrow at McLeansboro, Ill. Hatching success declined slightly with advancing season, but the differences were small. Fledging success decreased considerably with advancing season with the highest survival in clutches initiated during March and April and lowest in clutches initiated in June.

Adult Mortality Rate.—Mortality rates and population sizes of the two sparrows near Portage des Sioux were computed from data obtained from banded birds. During the course of the study, 2,505 sparrows were banded, 1,869 house sparrows and 636 tree sparrows. There were 376 live recaptures of house sparrows and 10 recoveries of dead house sparrows (3 from outside the study area). There were 135 recaptures of live tree sparrows and 4 recoveries (2 from outside the study area).

Equations presented by Haldane (1955) and Farner (1955) were used to compute the mortality rates of adult sparrows. Only birds from site B were used in the analyses because banding operations were performed regularly during the course of the study only at that site.

All adult sparrows captured during the breeding seasons of 1968-1974 were used to compute mean annual survival rates using Haldane's equation.

The data used in this analysis are summarized in Tables 16 and 17. The mean annual survival rate of adult house sparrows was 41.5% (s=3.31) and that of adult tree sparrows was 33.4% (s=5.14). The mean annual mortality rates of adult house sparrows and tree sparrows were therefore 58.5% and 66.6% respectively.

The method of Farner (1955) was also used to estimate the mean annual mortality rates of the two species. In this method the age composition of a population, determined in this study by recaptures in a relatively brief time period, is used to compute the mortality rate. Farner's Equation 4 was modified slightly due to the unequal amount of banding activity in different years of the study:

$$m = \frac{\Sigma(n_i/N_i \cdot 100)}{\Sigma\, 100i \cdot (n_i/N_i)}$$

where m=mean annual mortality rate, n_i=number recaptured from age class i and N_i=number originally assigned to age class i. Age classes were based on all individuals known to be alive on 1 September of the year. The principal assumption underlying the utilization of this equation is that the population is stable. This assumption appears to be justified for the house sparrow at site B (see below), but the tree sparrow population was expanding during the first three years of the study. The implications of this fact will be discussed below. Two house sparrow samples and one tree sparrow sample were used to compute mean annual mortality rates according to this equation.

Mortality rates of both species were computed on adult sparrows captured at site B during the 1972 breeding season. There were 38 adult house sparrows recaptured and 19 tree sparrows. The mean annual mortality rate of the house sparrow was 49.4% and that of the tree sparrow was 58.5%

The second house sparrow sample was 37 individuals recaptured during January 1972. The mean annual mortality rate computed from this sample was 50.6%.

The mean annual mortality rate of the house sparrow near Portage des Sioux is apparently lower than that of the tree sparrow, therefore. The fact that the tree sparrow population at site B was increasing rapidly during the early years of the study (see below) might have had some influence on this difference. Farner's equation, which depends on the assumption that the population is stable, would tend to over-estimate the mortality rate in an expanding population, due to the large number of young individuals presumably being added in a growing population. This fact would not account for the difference in mortality rates computed by the Haldane equation, however. Therefore, it would appear to be best to conclude that the adult mortality rate of the tree sparrow is somewhat higher (about 8%) than that of the house sparrow near Portage des Sioux.

Population Size.—Banding data were also used to estimate the size of the breeding population of the house sparrow at site B. It quickly became apparent that sparrows learn to avoid mist nets after being captured in them, and therefore captures made by that means were not random samples of the population. The effect of this nonrandomness is apparent in population size estimates using the Lincoln Index (see Southwood, 1966): 1969–88; 1970–220; 1971–351; 1972–495; 1973–512. Adults captured at a nest site served as one sample, and birds captured in mist nets served as the second sample. No mist nets were used prior to the 1969 breeding season so that this estimate is essentially unbiased. However, in subsequent years, avoidance of the mist nets by previously netted birds doubtless influenced the estimates. During the breeding seasons 1970-1973, for example, 40 (58.0%) of the 69 individuals captured at nest sites were previously banded, while only 60 (36.6%) of the 164 individuals captured in mist nets were previously banded. This difference is highly significant ($X^2=9.091$, $P<0.01$). This supports the conclusion that the capture probability of birds previously captured in mist nets is lower than the probability of capture of previously uncaptured birds.

Another method was required therefore to estimate the size of the breeding population of the house sparrow at site B. The method employed is based on the minimum breeding population size of the tree sparrow at site B as determined by concurrent occupancy of nest-boxes. As mentioned earlier, virtually all tree sparrows breeding at site B used nest-boxes for nest sites, so that the maximum concurrent occupancy would yield a minimum estimate of the number of pairs breeding at site B. The figures for the five years have been given previously, and are presented again in Table 18. The following proportion can then be used to estimate the minimum number of house sparrows breeding at site B:

$$\frac{n_h}{N_h} = \frac{n_t}{N_t}$$

where n_h and n_t are the numbers of house sparrows and tree sparrows, respectively, captured in mist nets at site B during the breeding season and N_t is the population size of the tree sparrow as determined by nest-box occupancy. The equation can then be solved for N_h, an estimate of the minimum number of house sparrows breeding at site B. The principal assumption is that the capture probabilities of house sparrows and tree sparrows in mist nets are equal. If this assumption is not correct, the accuracy of the estimates for each year would be affected, but comparisons between different years could still be made.

The results are summarized in Table 18. The small tree sparrow sample in 1969 makes the estimate for that year rather unreliable. The estimates for the other four years are very close to each other. The fact that in two of these four years, 1970 and 1972, the number of adult house sparrows captured during the breeding season actually exceeded the estimates suggests that these minimum estimates are too low. Taken together with the 1969 estimate of 88 computed with the Lincoln Index (see above), these figures suggest that about 35-50 pairs of house sparrows bred at site B during the years of the study, and that no major change occurred in the size of the breeding population.

Adult Weight.—Data on the weight of adult sparrows are presented in Fig. 4. The mean weight of all adult house sparrows was 29.6 g ($n=561$, $s\bar{x}=0.079$), and the mean of all adult tree sparrows was 22.0 g ($n=136$, $s\bar{x}=0.103$). The mean weight of the house sparrow varied with both sex and season. Males were heavier during the winter months November-February, averaging about 30 g, but during the breeding season their weight declined steadily to a low of 28.2 g in July and August. The mean weight for all males from throughout the year was 29.7 g ($n=295$, $s\bar{x}=0.093$). Females weighed less than males during the winter months, but their weight increased markedly at the beginning of the breeding season so that they outweighed males. High female weights during the breeding season are sometimes attributed to the fact that many are undoubtedly carrying eggs (Kluyver, 1952). Apparently this increased weight is maintained throughout incubation, however, as the mean weight of 6 females captured during egg-laying was 31.4 g, and the mean weight of 27 females captured during the incubation of completed clutches was 30.9 g.

Seasonal changes in the mean weight of adult tree sparrows are difficult to interpret because the sex of many individuals was unknown. The maximum mean weight of all adult tree sparrows occurred during the winter, however (Fig. 4).

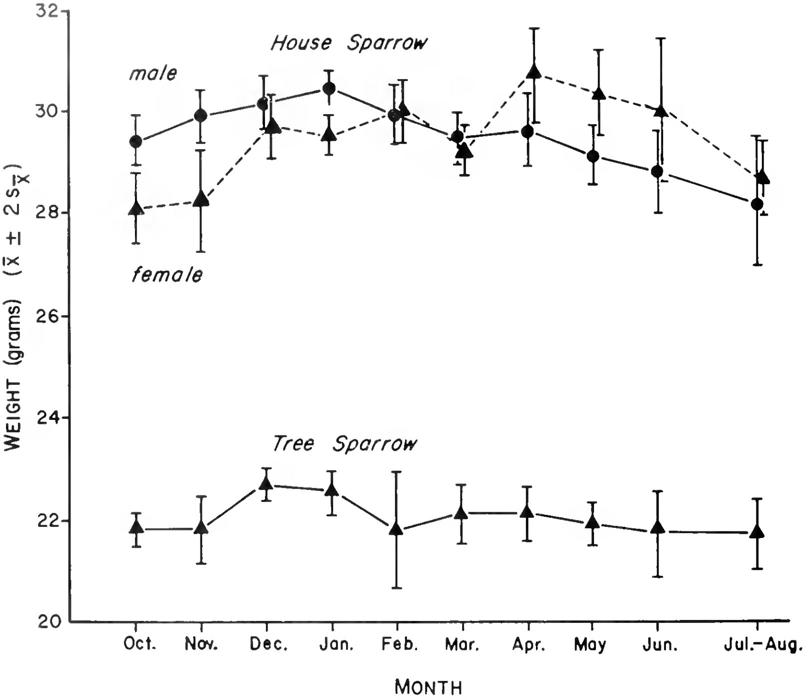

FIG. 4.—Seasonal changes in weight of adult house sparrows and tree sparrows near Portage des Sioux, Missouri.

Resource Utilization

Nestling Food.—Food samples were obtained from nestling house and tree sparrows during the 1971 breeding season. Samples were collected during the period 14 May to 14 August. Forty-nine samples were obtained from house sparrow nestlings, 53 samples from tree sparrow nestlings. The smaller number of samples collected for the house sparrow was due to the fact that some samples contained no food items.

A total of 1,145 items were identified, 364 from the house sparrow samples and 781 from the tree sparrow samples. The mean number of items per sample was 7.4 for the house sparrow and 14.7 for the tree sparrow. A breakdown of the nestling diets of the two species by weight and kingdom is presented in Table 19. These results are consistent with other reports of a high proportion of animal material in the diets of nestling sparrows (Kalmbach, 1940; Summers-Smith, 1963; Pinowski, 1968; Abé, 1970).

A list of all items identified from the samples is presented in Table 20. It is apparent from this list that the animal portion of the nestling diet of both species is comprised primarily of insects. The animal fraction of each diet also contained a small number of spiders and mites, the latter possibly inadvertently obtained as ectoparasites of other prey items rather than intentionally obtained as prey items themselves. The vegetable fraction consisted primarily of wheat kernels for the house sparrow, while the tree sparrow used a significant number of mulberries and miscellaneous seeds as well as wheat kernels. The grit present in small amounts in both diets consisted of snail shells and small stones. The vegetable fractions of both diets were comprised of items which were superabundant on the study area at the time of utilization by the sparrows. Subsequent analyses of the amount of overlap in the nestling diets of the two species therefore are concentrated on the animal fractions of the diets.

Adult insects in the samples were identified at least to family, and sometimes to subfamily, genus or species. In a few cases in which important parts of adult insects were missing, these were identified only to order. Larval insects were identified to order. Keys used were those in Brues *et al.* (1954), Essig (1958), Borror and White (1970) and Borror and DeLong (1971); the latter was used most, and nomenclature here follows that source.

An equation originally derived from information theory by Morisita and modified by Horn (1966) was employed to obtain an objective measure of the amount of overlap in the animal fractions of the nestling diets of the two sparrows. The equation provides a coefficient of overlap $C\lambda$, which has theoretical limits of 0 when there are no taxa in common, and 1.0 when there is complete correspondence of taxa and their percentages in the two diets.

The taxonomic units chosen for the purpose of obtaining a coefficient of overlap between the diets were family for adult insects and order for larval insects and arachnids. This somewhat arbitrary decision was based primarily on the fact that identifications of prey items were consistently made only to these taxonomic levels for the different age classes. Fifty taxonomic and age categories were represented in the combined sample, 26 of which were represented in the house sparrow samples, and 47 in the tree sparrow samples. For each category the percentage by weight of the total animal fraction of the diet of each species was obtained, and these values were used in computing the coefficient of overlap. The value of the coefficient was 0.9200, which indicates that the overlap in the two diets was very great. A similar study of the nestling diets of three sympatric blackbirds (Icteridae) in central Washington resulted in coefficients of overlap of 0.74, 0.79, and 0.82 for the three species combinations (Orians and Horn, 1969). Snelling (1968) also performed a similar study of the nestling diets of red-winged blackbirds *(Agelaius phoeniceus)* and common grackles at a common breeding site in Wisconsin, and reported an overlap of 0.52 using a different formula for the coefficient of overlap. Using the data reported in his paper a coefficient of overlap, $C\lambda$, was computed for the animal portions of the two diets. This recomputed coefficient of overlap was 0.4246.

To test whether or not there were temporal differences in the amount of overlap in the nestling diets of the two sparrows, the sampling period was divided into five subsample periods. This division was based partly on the distribution of samples, and time lengths are therefore unequal (see Table 21). A coefficient of overlap was computed for each temporal subsample in the same manner as described above except that the taxonomic units for which percentages were obtained were orders for both larval and adult arthropods. Table 21 gives the coefficients for each of the five subsamples. These coefficients of overlap are very high except for the last subsample period. Temporal overlap in the diets is particularly apparent when these coefficients are compared with coefficients of overlap computed between subsamples of the same species. These coefficients for the third and fifth subsamples are 0.4294 for the house sparrow and 0.7058 for the tree sparrow.

Lepidopteran larvae represented the largest category in the diets of both the house sparrow and the tree sparrow, constituting 47.9% and 46.9% respectively of the animal fractions of the diets. Although some species of lepidopterans were recognized in samples from both sparrows, there is no objective means of comparing more critically this portion of the nestling diets on the basis of taxonomic groups. In an attempt to discover whether or not the two species took different portions of the lepidopteran larva fauna, the size distributions of the larvae in the samples were compared. The mean length of the 105 larvae in the house sparrow samples was 17.4 mm, while the mean length of the 111 larvae in the tree sparrow samples was 17.7 mm. The difference is not significant ($t=0.323$, $P>0.70$).

Differences in the nestling diets of the two sparrows consist principally of omissions in the house sparrow samples of taxa utilized by tree sparrows (see Table 20). The absence of mulberries from the house sparrow samples has been noted previously. Mulberries were superabundant on the study area at the time that they were fed to tree sparrow nestlings, and there is no apparent reason why they would be avoided by house sparrows. A second major taxon in the tree sparrow diet which was missing from the house sparrow samples was adult ladybird beetles (Coccinellidae). Both species fed many coccinellid larvae and pupae to their young, but adult ladybird beetles were conspicuously absent from the house sparrow samples. Adult ladybird beetles were present in 41.5% of the tree sparrow samples, however, and constituted 9.74% of the animal portion of the diet by weight. This family of beetles is known to produce a noxious chemical which is distasteful to some predators (Rothschild, 1961), and the two species may respond differently to this substance. Coccinellid beetles have also been reported to be an important food item of the tree sparrow in Europe (Dornbusch, 1973).

A second major difference in the diets is that there are many more small items in the tree sparrow diet than in the house sparrow diet. Fig. 5 shows the frequencies by item length of all items in the samples of both species. This figure shows that above 7 mm there is generally close agreement between the two species, although the tree sparrow shows a slight numerical advantage between 8 and 15 mm, and the house sparrow shows a similarly slight advantage from 16 to 24 mm. Of the few items above 24 mm in length the tree sparrow again shows a greater number. Although the modal prey length for both species is 6 mm, the tree sparrow outnumbers the house sparrow (by a factor of about 2 to 8) in the size range from 1 to 7 mm. It would appear therefore that the tree sparrow is more efficient at obtaining small prey items.

Winter Food.—Observations at the feeding platform were made from January to March 1972. Unanticipated events, mainly the large numbers of sparrows feeding simultaneously, precluded the possibility of obtaining the expected quantitative results.

In mild winter weather (ambient temperature 0-5°C), the sparrows typically fed in bouts, with many individuals feeding on the tray simultaneously, followed by rather extended periods when no sparrows were feeding. Ten to 15 individuals of both species (in a ratio of about 5 house sparrows to 1 tree sparrow) constituted the normal group at the platform during a bout. In the very cold weather of 4 and 14 January (ambient temperature —15–18°C accompanied by high wind), however, I was unable to count the number of sparrows feeding simultaneously, but 30 would not be an unreasonable estimate. Feeding was also continuous on those days except when the birds were disturbed. Both species were observed in these congregations, but the ratio of tree sparrows to house sparrows could not be determined. There appeared to be fewer aggressive encounters in the very cold weather than during mild weather.

Two other species were observed at the feeding platform, the Carolina wren *(Thryothorus ludovicianus)* and the song sparrow. Scientific name of song sparrow given on page 12 of text—other scientific names not repeated. The Carolina wren fed alone, and was dominant over individual sparrows of both species. Several times the wren was observed to drive sparrows away from the platform by flying directly at them. However, the wren would soon be over-

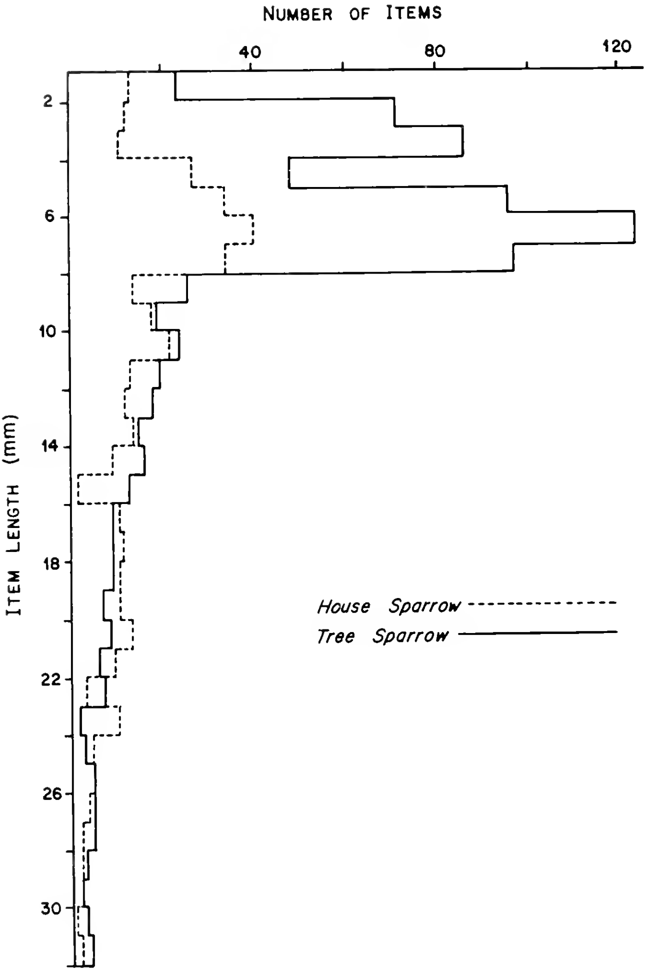

FIG. 5.—Frequency distributions by item length of nestling diets of house sparrows and tree sparrows.

whelmed by sheer numbers. Sparrows would alight on the platform faster than the wren could drive them away, and he would then leave. The song sparrow also attempted to exclude sparrows with threats (open beak display, for instance), but would feed in company with them when they became too numerous to exclude.

Group feeding has presumably evolved as a more efficient means of exploiting certain kinds of resources. Resources which are temporally and spatially clumped may be more effectively exploited by individuals of a species in which there is a reduction in the typical level of intraspecific aggressive behavior. These group feeders may gain access to a food resource against an opponent to which they are individually subordinate, as in the case of the sparrows and the Carolina wren. Brown (1971) reported a similar outcome in interactions between two chipmunk species, one of which succeeded in feeding in spite of its subordinate status because of its greater tolerance of other individuals and aggressive neglect by the dominant species.

Schoener (1972), in a review of foraging strategies, suggested that group feeding may arise selectively under three circumstances: (1) group feeding reduces foraging efficiency, but some other selective factor (i.e. predation) overrides this disadvantage; (2) group feeding results from the tendency of animals to aggregate in relation to the concentration of food and group size is selectively neutral; or (3) group feeding results in greater foraging efficiency. Group feeding in sparrows would clearly belong to the latter category, even extending it if, in fact, group feeding allows the sparrows to gain access to resources which they could not exploit individually.

Nest Sites.—The utilization by sparrows of the nest-boxes at site B during the 1969-1971 breeding seasons, prior to the enlargement of the entrance holes, was as follows: nest-boxes with a hole diameter of 29 mm—tree sparrow 44 seasons and house sparrow 1 season of a total of 53 seasons available; nest-boxes with a hole diameter ≧30 mm—tree sparrow 3 and house sparrow 20 of 26 available. Three conclusions can be drawn from these data: (1) utilization of the nest-boxes as nest sites by sparrows was extensive, (2) tree sparrows rarely used nest-boxes with entrance holes of sufficient diameter (≧30 mm) to allow utilization by house sparrows, and (3) house sparrows were virtually excluded from nest-boxes with an entrance hole diameter of less than 30 mm (house sparrows were twice found wedged into the entrance holes of these nest-boxes).

During the 1972 breeding season, after the enlargement of the entrance holes of 21 of the 27 nest-boxes with a hole diameter of 29 mm, all 36 nest-boxes were occupied by sparrows. The following categories of nest-boxes were recognized: (1) nest-boxes with a hole diameter equal to or greater than 30 mm for all years that they were present at site B, and hence always available to both species, (2) nest-boxes with hole diameter less than 30 mm for all years and hence available only to tree sparrows, and (3) nest-boxes in which the hole diameter was enlarged from less than 30 mm to greater than 30 mm in September 1971, thereby making them available to the house sparrow for the first time in 1972. The occupancy of these various categories of nest-boxes in 1972 is summarized in Table 22.

The occupancy of nest-boxes in category 1 was essentially like that in previous years. The ratio of 1 tree sparrow to 8 house sparrows is very similar to the 3 to 20 ratio in previous breeding seasons in the same nest-boxes. All six nest-boxes in category 2 were occupied by tree sparrows, also similar to the condition in previous years.

The occupancy of nest-boxes in category 3 is intriguing. At the beginning of the breeding season, tree sparrows occupied 11 and house sparrows 10 of the 21 nest-boxes. As the breeding season progressed, however, the tree sparrows lost possession of four of these boxes, one before the completion of the first clutch, two after one brood had been successfully fledged, and the fourth after three successful broods. One nest-box initially occupied by the house sparrow was later occupied by the tree sparrow . Thus the final occupancy ratio was 8 to 13, tree sparrow to house sparrow.

The difference between the 11 to 10 or 8 to 13 occupancy ratio in category 3 nest-boxes and the 4 to 28 combined ratio for category 1 nest-boxes from 1969-1972 requires some explanation. If all factors affecting the occupancy of category 3 nest-boxes were identical to the factors affecting category 1 nest-boxes, the occupancy ratios for the two categories should be equal. The difference between the 8 to 13 and 4 to 28 ratios is significant ($X^2=4.757$, $P<0.05$). The major difference between the two categories was that category 3 nest-boxes had been occupied in previous years only by tree sparrows (20 of the 21 were occupied by tree sparrows in 1971). Nest sites are first occupied during an autumnal period of sexual activity, and most birds then roost at their nest sites during the winter, thereby retaining possession. It is possible that adult tree sparrows which have utilized a nest site during the previous breeding season are able to exclude house sparrows, most of them young individuals, from these sites and retain possession for the next breeding season. Young tree sparrows would probably be at a disadvantage against the larger house sparrow, however, in contests for unoccupied sites. The 60% annual mortality rate of adult tree sparrows (see above) would leave half or more of their nest sites open to be occupied by new tenants, most of which would be house sparrows.

The occupancy of nest-boxes in 1973, also recorded in Table 22, tends to confirm this hypothesis. The 13 experimental nest-boxes that were in the possession of house sparrows at the end of the 1972 breeding season were considered to be in category 1, and only the 8 boxes that remained in the possession of tree sparrows at the end of the 1972 breeding season were considered to be in category 3. Twenty-one of the 22 nest-boxes in category 1 were occupied by house sparrows in 1973 (one remained unoccupied). The 8 nest-boxes in category 3 were divided evenly between house sparrows and tree sparrows. Nine new nest-boxes with a hole diameter of 29 mm were added prior to the 1973 breeding season bringing the total number of nest-boxes in category 2 to 15, 14 of which were occupied by tree sparrows in 1973.

CONCLUSIONS

The following ten statements summarize the results of this study. In this section each will be explained and further elaborated, and these findings will be used to attempt to answer the questions posed in the introduction. In addition, implications of these findings for current problems in population and community ecology will be discussed. The concept of the niche used in the following discussion is essentially that of Hutchinson (1957), with each resource being represented along some linear continuum. The entire niche of a species can then be visualized as a hypervolume in an n-dimensional space, where n is equal to the number of resources. The nest site niches and other niches discussed below are actually subniches within this hypervolume.

1. The house sparrow and the tree sparrow are syntopic during the breeding season.
2. The breading seasons of the two species overlap completely.
3. The nest site niche of the house sparrow virtually contains the nest site niche of the tree sparrow.
4. The house sparrow is more successful than the tree sparrow in procuring nest sites available to both species.
5. The nestling food niches of the two species overlap extensively, taxonomically and temporally.
6. The tree sparrow is more efficient than the house sparrow in procuring smaller items within the nestling food spectrum.
7. Tree sparrow fecundity exceeds house sparrow fecundity in all reproductive parameters examined.
8. Nestling survival in both species improves markedly in the latter part of the breeding season, coincident with a divergence in the nestling diets of the two species.
9. The winter feeding niches of the two species are very similar, with common, social feeding prominent.
10. Annual adult mortality rates of the two species are similar although the house sparrow apparently has a somewhat lower mortality rate than the tree sparrow.

Two species are said to be syntopic when they share the same habitat. This term therefore extends the concept of sympatry, in which two species coexist geographically, but do not necessarily occupy the same habitat within their area of geographic overlap. It is apparent from this study that the habitats of the house sparrow and the tree sparrow are essentially identical, particularly during the breeding season. Both species were common at site B during the study, and both species mixed thoroughly throughout site B in occupying nest sites. Further evidence for syntopy is the fact that tree sparrows failed to occupy nest-boxes put up in parkland and woodland edge habitats at site C. These habitats seemed to me to be very similar to habitats described by Pinowski (1968) as commonly occupied by the species in Poland, and this impression was confirmed by Pinowski on a visit to the site in early 1975 (Pinowski, pers. comm.). Lack (1971) reported that the two species are separated by habitat in Europe.

The breeding seasons of the two species are also coincident. Both species are multi-brooded and their breeding activities extend from the first or middle part of April to the first part of September. This temporal coincidence is apparent in the overlap in clutch initiation for the years 1969-1973 (Fig. 6). The only difference between the breeding seasons of the two species is the approximately 10 day later start of the tree sparrow.

The habitat syntopy during the breeding season and the temporal coincidence of the breeding seasons mean that the two species must extract the resources necessary for reproduction from the same habitat at the same time. Two of the most important resources associated with reproduction are space (primarily nest sites in these colonial, hole-nesting species) and energy (represented in this study by the food fed to nestlings).

House sparrows utilized many types of nest sites during this study, most commonly crevices in buildings, natural cavities in trees, open sites in the branches of trees and nest-boxes. Tree sparrows, however, used nest-boxes almost exclusively, although natural cavities in trees were also used, and probably constitute the principal nest sites in the absence of nest-boxes. Except for the nest-boxes constructed specifically to exclude the house sparrow, therefore, the nest site niche of the tree sparrow is apparently completely contained within the nest site niche of the house sparrow.

The occupancy ratio of tree sparrows to house sparrows in the nest-boxes that were available to both species for the entire duration of the study was 4 to 37. This contrasts sharply with the 64 to 2 occupancy ratio in nest-boxes with a hole diameter sufficiently small to virtually exclude the house sparrow. This strongly suggests that the house sparrow is more successful than the tree sparrow in obtaining nest sites. Further evidence for this conclusion is supplied by the occupancy of nest-boxes in which the entrance holes were enlarged in September 1971. During the 1971 breeding season, 20 of these 21 nest-boxes were occupied by tree sparrows. At the end of the 1972 breeding season, however, 13 of the 21 were occupied by house sparrows, and only 8 by tree sparrows. Of these 8, only 4 remained

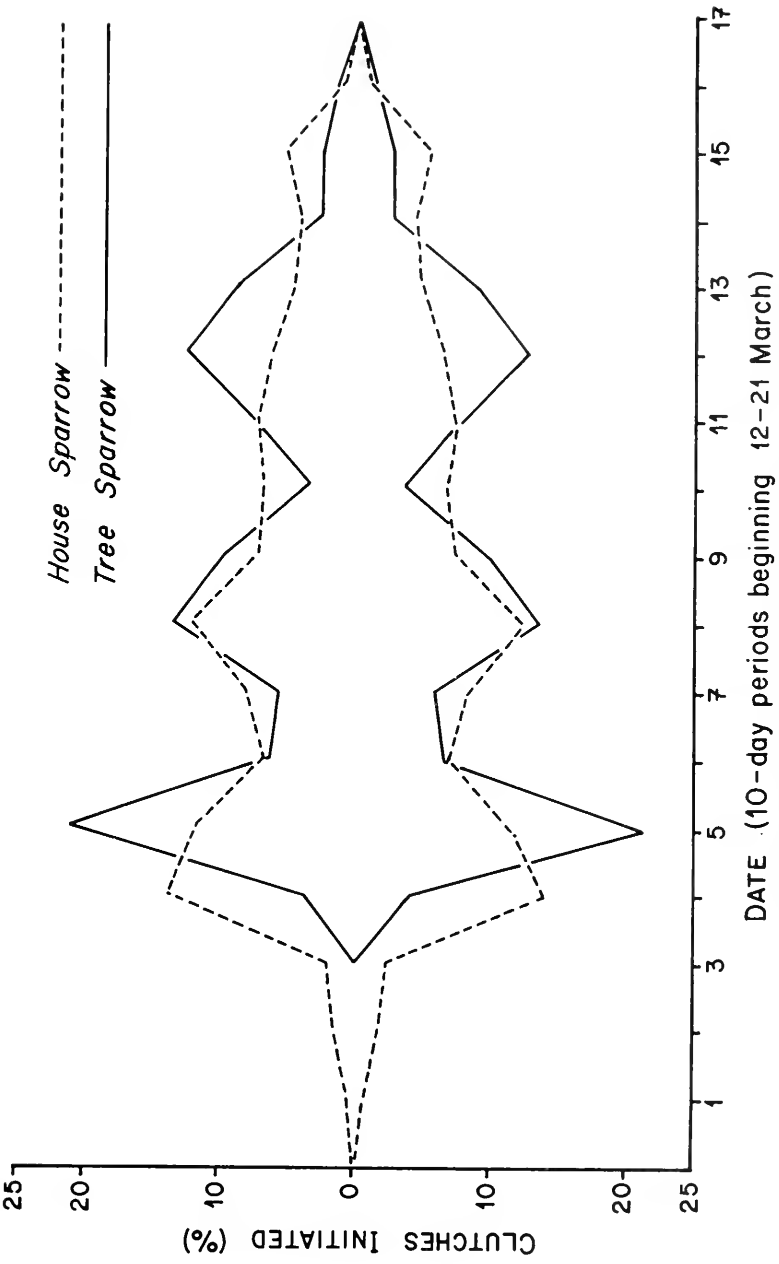

Fig. 6.—Temporal overlap in the breeding seasons of the house sparrow and tree sparrow near Portage des Sioux, Missouri, 1969-1973.

in the possession of tree sparrows in 1973, and the remaining 4 were held by house sparrows.

Although both species are granivorous outside the breeding season, they feed their nestlings primarily insects. The taxonomic compositions of the animal portions of the nestling diets of the two species were very similar, as evidenced by the coefficient of overlap of 0.9200. This figure is higher than that found in any two-species comparison of nestling diets which could be found in a search of the literature. Temporally, the diets were also very close, being very similar in May, June and early July, but less similar in late July and August. The evidence, however, supports the generalization that the nestling diets of the two species are essentially identical, both taxonomically and temporally.

In exploiting these common resources to provide food for their nestlings, the tree sparrow is more successful than the house sparrow in obtaining items at the smaller end of the resource spectrum. This is suggested by the fact that in an approximately equal number of nestling food samples, the numbers of items above 7 mm in length taken by each species were about equal, but in the size range 7 mm and less, the tree sparrow outnumbered the house sparrow by a factor varying from about 2 to 8.

The fecundity of the tree sparrow was greater than that of the house sparrow for each fecundity parameter examined (Table 23). The resultant difference in fecundity, expressed as number of young fledged per pair-season favored the tree sparrow by a factor of 1.49. The mean number of young fledged per pair-season was 4.52 for the house sparrow and 6.74 for the tree sparrow. At Oxford the house sparrow fledged 2.9 young per pair-season and the tree sparrow fledged 3.9 (Seel 1970).

Fledging success increased significantly in both species in the latter part of the breeding season. This coincided with the divergence in the nestling diets mentioned above (see Table 21), and is illustrated in Fig. 7. A decrease in fledging success with advancing season seems to be more common in birds (Lack 1966), and this was found to be true for the house sparrow at McLeansboro, Illinois (Will 1969). A significant increase in fledging success in the latter part of a prolonged breeding season appears to be rare in birds, and the presence of this increase in both of these species coincident with a divergence in their nestling diets is of considerable importance, and will be discussed further below.

The winter feeding niches of these two species are apparently very similar. Foraging flocks comprised of both species were commonly observed. At the feeding platform both species fed together, with larger groups feeding simultaneously in severe weather than in mild weather. No marked differences in intraspecific and interspecific aggressive encounters in the two species were noted.

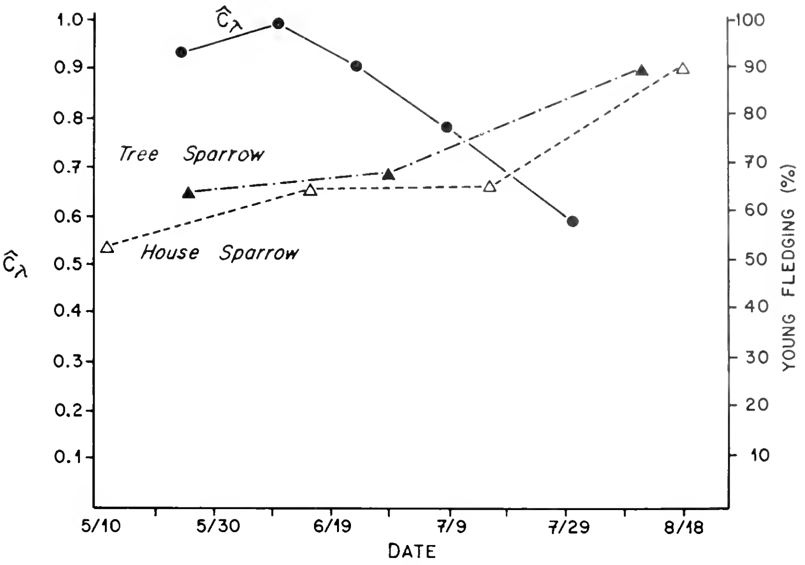

FIG. 7.—Fledging success of the house sparrow and tree sparrow plotted against nestling food overlap.

The estimates of annual mortality rate of adult house sparrows were 58.5%, 49.4% and 50.6%: and the estimates of annual mortality rate of adult tree sparrows were 66.6% and 58.5%. These estimates suggest that the mortality rates of the two species are similar, although that of the house sparrow is probably about 8% lower than that of the tree sparrow.

Interspecific competition has been defined as the utilization by two species at the same trophic level of resources which are actually or potentially limiting to one or both of the species (Miller 1967). Two problems are encountered in attempting to operationalize this definition. The first is to arrive at an acceptable definition of "limiting." In this discussion the classical definition of Blackman (1905) will be used, as described below. The second is to identify resources which are "potentially" limiting. One must find a situation in which these resources are actually limiting before they can be identified with certainty. The word "potentially" therefore has little meaning in the operational definition, especially when the application is to a natural system and not to a laboratory system.

The classical Lotka-Volterra equations for a two-species system will be used to attempt to illustrate the concept of limiting factors as it relates to this discussion:

$$\frac{dN_1}{dt} = r_1N_1\left(\frac{K_1 - N_1 - \alpha N_2}{K_1}\right)$$

$$\frac{dN_2}{dt} = r_2N_2\left(\frac{K_2 - N_2 - \beta N_1}{K_2}\right)$$

Where N is the number of individuals (subscripts refer to species 1 and species 2), t is time, r is the intrinsic per capita rate of increase (the difference between the per capita birth rate and the per capita death rate), K is the carrying capacity of the environment for the species, and α and β are coefficients relating the impact of one species on the other species. The carrying capacity of the environment is related to the fact that the environment of any species contains a finite supply of resources upon which the species depends, and these resources set a limit on the number of individuals of the species that can reside there. The term in brackets in these equations then describes the modification of the intrinsic rate of increase of a species imposed by the reduction of limiting resources by the presence of individuals of that species and/or of the second species. Limiting resources would then be those resources which, when reduced by an increased number of individuals of a species or its competitor, would cause a decrease in the per capita birth rate or an increase in the per capita death rate of the species.

In addition to the above definitions, the terms "ecological time" and "evolutionary time" will be used in the following discussion. Ecological time refers to the time frame of succession in temperate zone ecosystems, approximately 100-500 years (Odum, 1971). Evolutionary time refers to the speciation time of macroorganisms, a minimum of 10,000 years in birds (Selander, 1971). Thus there are about two orders of magnitude difference between ecological and evolutionary time.

"Are there competitive interactions between the house sparrow and the tree sparrow in North America?" It seems clear from the above observations that the answer to this question is yes. Nest sites and nestling food are two resources that are shared by the two species. This study provides strong evidence that nest sites are a limiting resource, at least for the tree sparrow. The marked increase in the breeding population at site B from 1969 to 1971 followed the provision of additional nest sites in the form of nest-boxes. The decrease in occupancy during the 1972 breeding season when most of the nest-boxes were made available to both species, further substantiates the fact that nest sites are a limiting resource for this species. The food fed to nestlings has long been presumed to be a limiting resource in reproduction (Lack, 1948, 1954, 1968; Cody, 1966), but evidence supporting this belief is primarily indirect (see Cody, 1971). The increase in nestling survival late in the breeding season coincident with the divergence in the nestling diets constitutes strong evidence for the proposition that food is, in fact, limiting recruitment in these species. If this is the case, fledging success in the house sparrow should have been affected by the changing size of the breeding population of the tree sparrow during the study. Table 24 summarizes the results of comparing hatching and fledging success in the house sparrow at site B for the low density years of the tree sparrow (1968-1970) with success in the higher density years (1971-1973). Hatching success in both the low density and high density years was identical, 68.6%, but fledging success in the high density years (59.7%) was significantly lower than in the low density years (73.8%) ($X^2=23.769$, $P<0.001$). The greatest disparity in fledging success rates between the two samples was for clutches initiated during the first part of the breeding season, 17 March-10 May, and the unusually poor fledging success during that period in 1973 due to the early start and subsequent cold spell mentioned earlier could be biasing the analysis independent of the tree sparrow density. Therefore, combined fledging success rates of the last three periods were compared, and the difference between the high density and low density years was still significant in the direction anticipated ($X^2=4.273$, $P<0.05$). This study also suggests that the winter food is a shared resource, but no direct evidence that it is actually limiting one or both species was obtained.

Because the answer to the first question is affirmative, the second must also be answered. "What interactions may be involved in limiting the distribution of the tree sparrow in North America?" Of the two areas of competition identified during this study, nest sites would appear to be the more critical for the tree sparrow. The decrease in the minimum breeding population size of the tree sparrow at site B in 1972 can be directly attributed to the fact that all nest-boxes were occupied, and fewer nest-boxes were exclusively available to tree sparrows. The number of nest sites occupied by the tree sparrow actually decreased during the breeding season as well, as more sites available to both species were appropriated by house sparrows. These observations supplement the earlier observations of Widmann (1889), and suggest that recruitment in the tree sparrow may be severely reduced by the appropriation of potential nest sites by house sparrows. The tree sparrow appears to be at an advantage in exploiting the common nestling food niche of the two species, however. Broods are larger and fledging success is consistently higher than in the house sparrow.

The third question in the introduction should perhaps be modified to ask, "How does the tree sparrow persist in the face of competition from the house sparrow?" The picture that emerges from this study is that the house sparrow is firmly entrenched astride the niche of the tree sparrow. It is possible, however, that the persistence of the tree sparrow is directly related to its high fecundity and its superior ability to exploit food resources to fuel this high reproductive effort. The rapid expansion of the population at site B during the study offers an example of this ability. In the terminology of MacArthur and Wilson (1967), the tree sparrow would therefore be an r-selected species. This existence would seem to be somewhat tenuous; and, in fact, rapid and inexplicable changes in the population size of the species have been noted in England (Alexander and Lack, 1944, cited in Seel, 1968a) as well as in the United States (Barlow, 1973).

It should be apparent that this study has not provided final answers to the questions posed in the introduction. The questions asked were not necessarily exhaustive either. For instance, questions could have been posed concerning the possibility that reduced genetic variability in the small founding population of the tree sparrow (20 individuals) could have seriously reduced its potential for adaptation on this continent. Questions could also have been posed concerning the impacts of predation and/or parasitism on the tree sparrow in North America.

It does seem clear, however, that the presence of the house sparrow has probably been an important factor in limiting the success of the tree sparrow in North America. Competition occurs between the two species for important resources (nest sites, nestling food and possibly winter food). The house sparrow exploits the common nest site niche more efficiently than the tree sparrow, probably because of its larger size and its 10 day earlier initiation of breeding. The resulting prevention of an opportunity to breed may make this the most severe limiting factor for the tree sparrow in North America. The fact that this competition has not resulted in the complete disappearance of the tree sparrow from North America seems to raise questions about the validity of the principle of competitive exclusion, at least in its usual application to species distributions in an ecological time reference.

The principle of competitive exclusion was theoretically derived from the Lotka-Volterra equations and experimentally demonstrated in laboratory populations of *Paramecium* by Gause (1934). Where two species compete for the same resource, "one of the species in a mixed population drives out the other entirely" (Gause, 1934, 113).

The results of the present study appear to parallel the results of field experiments on three salamanders in the genus *Ambystoma* which coexist in ponds in southeastern Michigan (Wilbur, 1972). The experiments demonstrated that all three species compete significantly with each other, but exclusion is not the outcome of this competition. Wilbur concluded that this evidence did not negate the principle of competitive exclusion, which adequately describes the outcome of competition between two species for one resource in a simple laboratory system. Instead, he concluded that the structural complexity and temporal diversity of the pond community represent a higher order system than the deterministic laboratory system. Therefore, in spite of competition for limiting resources, the three species continue to coexist "due to the presence of good years and good ponds for each species" (Wilbur, 1972:17).

The sparrows in this study and the salamanders of Michigan ponds suggest that exclusion is not the necessary outcome of interspecific competition in natural systems, at least in an ecological time reference (the sparrows have coexisted for almost 100 years in North America). Therefore, although the principle of competitive exclusion does appear to apply in many situations (see Brown, 1971; Heller, 1971; Sheppard, 1971; Jaeger, 1971, 1972), its application to natural systems is not universal, justifying the skepticism of its critics (see Cole, 1960; Andrewartha, 1961; Peters, 1976). Miller (1969) has suggested that the principle may not apply in the same way to systems in which competition takes different forms. In natural systems in which the limiting resources occur in a form which favors competition by interference (i.e., resources can be economically defended, and therefore interspecific territorial systems can be developed (see Brown, 1964)), divergence in resource utilization or exclusion of one species by another will frequently occur. However, in systems where resources are distributed in such a way that competition takes the form of exploitation, exclusion of one species by another may be rare, and convergence rather than divergence will be favored.

The results of this study point to the fact that the usual application of the principle of competitive exclusion to species distributions in an ecological time reference needs re-thinking. Competing species do coexist in nature. Under the influence of this competition, it would seem that natural selection would reduce the amount of niche overlap between the competing species, resulting ultimately in niche differentiation. However, it seems equally apparent that competition cannot be invoked to explain both the limitation of animal distributions in ecological time, and the structure of biotic communities in evolutionary time. The niches of two species cannot diverge adaptively under the influence of competitive interactions unless the two species can coexist in ecological time. Unless the two species coexist, there would be no force at work to cause the adaptive changes.

SUMMARY

Concurrent population studies of the house sparrow *(Passer domesticus)* and the European tree sparrow *(Passer montanus)* were initiated in June 1968 at a study area near Portage des Sioux, Missouri. These studies continued through September 1973. Coincident with the population studies, the interactions between the two species over certain resources were examined: nestling food, nest sites and winter food.

The breeding seasons of the two species overlapped almost completely at Portage des Sioux. The fecundity of the tree sparrow was greater than that of the house sparrow for each fecundity parameter examined. As a result, the mean number of young fledged per pair-season was 4.52 for the house sparrow and 6.74 for the tree sparrow. The mean annual adult mortality rate of the house sparrow was found to be about 54%, approximately 8% less than that of the tree sparrow.

The nestling food niches of the two species were found to be very similar, with a coefficient of overlap, $C\lambda$, of 0.9200 for the animal fractions of the diets. Temporally, the nestling diets were very similar during the early and middle parts of the breeding season, but diverged somewhat during the latter part. This divergence in nestling diets coincided with significantly increased fledging rates in both species.

The house sparrow utilized a variety of nest site types, but the tree sparrow used only nest-boxes and holes in trees. The nest site niche of the tree sparrow was therefore completely contained within the nest site niche of the house sparrow, and the house sparrow was more successful in obtaining nest sites that were available to both species, probably due to its larger size and its 10 day earlier initiation of breeding.

Interspecific group foraging was observed during the winter, and apparently the two species shared a common winter food resource.

It was concluded that the two species were in competition for food and nest sites during the breeding season. The nest site competition was particularly detrimental for the tree sparrow, and might constitute a major limiting factor for the species. However, the tree sparrow appeared to be more successful than the house sparrow in utilizing items at the small end of the nestling food spectrum, and its higher fecundity might be the result of this fact.

The results of this study present a challenge to the usual application of the principle of competitive exclusion to species distributions in ecological time. Competing species do continue to coexist. Such

relationships may be unstable (non-equilibrial), but may persist because of the complexity and temporal diversity of the community. Adaptive changes would then accumulate in the species under the selective pressure of this competition, and ultimately the species would diverge in their resource requirements, with the result that the community would become more stable. Such adaptive divergence would be impossible, however, without the coexistence of competing species in ecological time.

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Appendix—Tables Referred to in the Text

Table 1.--Duration of the breeding seasons of the house sparrow and the tree sparrow near Portage des Sioux, Missouri, 1968-1974.

Year	1968	1969	1970	1971	1972	1973	1974	$\bar{x}$	$s_{\bar{x}}$
House Sparrow									
# of Clutches	-	90	109	124	168	194			
First Clutch	-	4/10	4/8	3/17	4/14	3/18	3/17	3/30	5.5
Last Clutch	8/8	8/14	8/8	8/7	8/9	8/13	-	8/10	1.2
Duration (days)	-	127	123	143	118	149	-	132	6.0
Tree Sparrow									
# of Clutches	-	11	29	73	59	58	-		
First Clutch	-	4/26	4/21	4/18	4/16	4/22	4/15	4/20	1.7
Last Clutch	-	7/26	8/6	8/7	8/12	8/13	-	8/7[1]	3.2
Duration (days)	-	92	108	112	119	114	-	109[1]	4.6

[1] If the small 1969 sample is ignored, last clutch $\bar{x}$ = 8/10, duration $\bar{x}$ = 113.

Table 2.--Clutch initiation-hatching intervals of the house sparrow and the tree sparrow near Portage des Sioux, Missouri, 1968-1973.

Clutch Size	Clutch Initiation	n	Clutch Initiation-Hatching Interval (Days) Range	$\bar{x}$	$s_{\bar{x}}$
House Sparrow					
c/2,3,4	3/17 - 5/10	1	14	(14)	-
	5/11 - 8/14	10	11-15	12.9	0.38
c/5,6	3/17 - 5/10	22	13-16	14.8	0.20
	5/11 - 8/14	49	12-17	14.1	0.13
Total		82	11-17	14.1	0.12
Tree Sparrow					
c/4,5	4/16 - 5/20	6	14-17	15.3	0.42
	5/21 - 8/13	19	13-15	14.1	0.13
c/6,7	4/16 - 5/20	5	16-18	16.8	0.37
	5/21 - 8/13	5	14-17	15.2	0.58
Total		35	13-18	14.9	0.21

Table 3.--Clutch initiation-hatching intervals of the house sparrow and the tree sparrow for clutches of five eggs.

		Clutch Initiation-hatching Interval		
Species	n	Range	$\bar{x}$	$s_{\bar{x}}$
House Sparrow	49	12-17	14.2	0.13
Tree Sparrow	21	13-17	14.5	0.19

Table 4.--Clutch initiation-fledging intervals and nestling periods of the house sparrow and the tree sparrow near Portage des Sioux, Missouri, 1968-1973

	House Sparrow	Tree Sparrow
Number	66	15
Mean Clutch Initiation-fledging Interval (S.E.)	28.9 (0.20)	28.9 (0.56)
Mean Clutch Initiation-hatching Interval	14.1 days	14.9 days
Nestling Period	14.8 days	14.0 days

Table 5.--Number of clutches initiated per nest site per season for the house sparrow and tree sparrow near Portage des Sioux, Missouri, 1969-1973.

	House Sparrow		Tree Sparrow	
Year	$\bar{x}$	S. E.	$\bar{x}$	S. E.
1969	2.09	0.166	1.83	0.401
1970	2.06	0.136	1.93	0.267
1971	2.14	0.144	2.70	0.225
1972	2.37	0.157	3.11	0.215
1973	3.23	0.197	2.76	0.300
Total	2.40	0.077	2.61	0.128

Table 6.--Clutch size of the house sparrow and the tree sparrow near Portage des Sioux, Missouri, 1968-1973.

	House Sparrow			Tree Sparrow		
Year	n	$\bar{x}$	S. E.	n	$\bar{x}$	S. E.
1968[1]	36	4.14	0.121	-	-	-
1969	85	4.60	0.067	9	5.33	0.408
1970	97	4.60	0.091	25	5.40	0.163
1971	112	4.68	0.084	66	4.83	0.091
1972	154	4.62	0.076	54	4.96	0.150
1973	172	4.68	0.066	52	4.96	0.099
1969-1973	620	4.64	0.035	206	4.99	0.062

[1] Data collected for portion of year only (June-August).

Table 7.--Summary of hatching success of the house sparrow near Portage des Sioux, Missouri, 1968-1973.

Fate of Clutch	Number of Clutches (Per Cent)	Number of Eggs Lost (Per Cent)	Per Cent of Eggs Laid
Clutches lost prior to completion	45(6.9)	76(7.4)	2.6
Complete clutches in which all eggs were lost or failed to hatch	103(15.8)	439(42.9)	15.2
Clutches in which at least one egg hatched, but all did not	308(47.2)	509(49.7)	17.6
Clutches in which all eggs hatched	197(30.2)		
Total	653(100.1)	1024(100.0)	35.4

Table 8.--Summary of hatching success of the tree sparrow near Portage des Sioux, Missouri, 1969-1973.

Fate of Clutch	Number of Clutches (Per Cent)	Number of Clutches (Per Cent)	Per Cent of Eggs Laid
Clutches lost prior to completion	17(7.9)	36(12.2)	3.5
Complete clutches in which all eggs were lost or failed to hatch	24(11.1)	116(39.5)	11.3
Clutches in which at least one egg hatched, but all did not	98(45.4)	142(48.3)	13.8
Clutches in which all eggs hatched	77(35.6)		
Total	216(100.0)	294(100.0)	28.6

Table 9.--Summary of examinations of eggs that failed to hatch.

Species	Infertile	Embryonic Death			Addled	N
		Early	Mid	Late		
House Sparrow	47(32%)	61(42%)	9(6%)	14(10%)	14(10%)	145
Tree Sparrow	20(37%)	15(28%)	1(2%)	6(11%)	12(22%)	54

Table 10.--Summary of hatching success of the house sparrow in nest-boxes, 1969-1973.

Fate of Clutch	Number of Clutches (Per Cent)	Number of Eggs Lost (Per Cent)	Per Cent of Eggs Laid
Clutches lost prior to completion	14(5.9)	23(6.6)	2.0
Complete clutches in which all eggs were lost or failed to hatch	32(13.6)	144(41.3)	12.9
Clutches in which at least one egg hatched, but all did not	113(47.9)	182(52.1)	16.3
Clutches in which all eggs hatched	77(32.6)		
Total	236(100.0)	349(100.0)	31.2

Table 11.--Summary of fledging success of the house sparrow near Portage des Sioux, Missouri, 1968-1973.

Fate of Brood	Number of Broods (Per Cent)	Number of Young Lost (Per Cent)	Per Cent of Young Hatched
All young died prior to fledging	117(23.1)	395(57.6)	21.4
At least one young fledged, but all did not	182(36.0)	291(42.4)	15.8
All young fledged successfully	207(40.9)		
Total	506(100.0)	686(100.0)	37.2

Table 12.--Summary of fledging success of the tree sparrow near Portage des Sioux, Missouri, 1969-1973.

Fate of Brood	Number of Broods (Per Cent)	Number of Young Lost (Per Cent)	Per Cent of Young Hatched
All young died prior to fledging	17(10.1)	77(39.3)	10.9
At least one young fledged, but all did not	80(47.3)	119(60.7)	16.8
All young fledged successfully	72(42.6)		
Total	169(100.0)	196(100.0)	27.7

Table 13.--Summary of fledging success of the house sparrow in next-boxes, 1969-1973.

Fate of Brood	Number of Broods (Per Cent)	Number of Young Lost (Per Cent)	Per Cent of Young Hatched
All young died prior to fledging	38(21.0)	150(56.8)	21.6
At least one young fledged, but all did not	78(43.1)	114(43.2)	16.4
All young fledged successfully	65(35.9)		
Total	181(100.0)	264(100.0)	38.0

Table 14.--Summary of breeding success of the house sparrow near Portage des Sioux, Missouri, 1968-1973, with temporal breakdown of hatching and fledging success.

Date of Clutch Initiation	Hatching Success (S_h)	Fledging Success (S_f)	Breeding Success (S_h X S_f)
Mar. 17 - May 10	65.2%	52.9%	34.5%
May 11 - June 9	62.7%	64.3%	40.3%
June 10 - July 9	69.4%	65.6%	45.5%
July 10 - Aug. 14	58.3%	89.0%	51.9%
Total	64.6%	62.8%	40.6%

Table 15.--Summary of breeding success of the tree sparrow near Portage des Sioux, Missouri, 1969-1973, with temporal breakdown of hatching and fledging success.

Date of Clutch Initiation	Hatching Success (S_h)	Fledging Success (S_f)	Breeding Success (S_h X S_f)
Apr. 16 - May 20	73.4%	64.6%	47.4%
May 21 - June 24	70.1%	67.3%	47.2%
June 25 - Aug. 13	70.7%	88.9%	62.9%
Total	71.5%	72.4%	51.8%

Table 16.--Summary data on last recapture of house sparrows captured at least once during the breeding season (March 16 - August 15) at site B, used to compute mean annual survival according to the formula of Haldane (1955).

						x			
Year Class	k	n_k	1	2	3	4	5	6	7
1967	7	2	1	1	0	0	0	0	0
1968	6	38	20	11	1	4	2	0	
1969	5	59	41	3	11	4	0		
1970	4	38	26	9	1	2			
1971	3	60	42	6	12				
1972	2	40	30	10					
1973	1	41	41						
		278	201	40	25	10	2	0	0
						d_x			

$s = 0.415$ (s.e. = 0.0331)

Table 17.--Summary of data on last recapture of tree sparrows captured at least once during the breeding season (March 16-August 15) at site B, used to compute mean annual survival according to the formula of Haldane (1955).

Year Class	k	n_k	x					
			1	2	3	4	5	6
1968	6	8	5	1	2	0	0	0
1969	5	17	7	7	2	1	0	
1970	4	27	15	11	1	0		
1971	3	21	19	2	0			
1972	2	14	12	2				
1973	1	4	4					
		91	62	23	5	1	0	0
			d_x					

$s = 0.334$ (s. e. $= 0.0514$)

Table 18.--Minimum breeding population sizes of the house sparrow and the tree sparrow at site B near Portage des Sioux, Missouri, 1969-1973.

Year	Minimum # of Occupied Nest-boxes	N_t	n_t (Total captured)[1]	n_h (Total captured)[1]	N_h
1969	4	8	1(8)	20(37)	160
1970	9	18	15(19)	50(67)	60
1971	22	44	23(28)	27(39)	52
1972	17	34	27(31)	55(71)	69
1973	17	34	16(18)	32(50)	68

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[1] Includes all adults captured during the breeding season at site B, most of those not captured in mist nets were captured at nest sites.

Table 19.--Summary of results of comparative nestling food study of the house sparrow and the tree sparrow near Portage des Sioux, Missouri, 1971.

	House Sparrow	Tree Sparrow
Number of Samples	49	53
Total Number of Items	364	781
Number of Taxa Represented	26	47
Per Cent of Diet by Weight		
Animal	78.4	82.3
Vegetable	20.0	16.1
Grit	1.7	1.6

Table 20.--Itemized list of food fed to nestling house sparrows and tree sparrows, 1971.

Food Taxon	Per Cent Occurrence		Number of Items		Weight (mg)	
	House Sparrow	Tree Sparrow	House Sparrow	Tree Sparrow	House Sparrow	Tree Sparrow
ANIMAL KINGDOM						
Arthropoda						
Arachnida						
Acari	16.3	3.8	13	3	+	+
Araneida	8.2	20.8	5	15	42.9	55.0
Insecta						
Orthoptera						
Acrididae	22.4	18.9	17	12	681.8	166.5
Tettigoniidae	16.3	5.7	8	4	256.6	42.8
Gryllidae	2.0	3.8	1	2	9.7	80.0
Hemiptera						
Miridae		3.8		3		7.1
Miris sp.		1.9		3		4.2
Lygus sp.		3.8		2		2.8
Lygus lincolaris		1.9		1		2.3
Nabidae		1.9		1		4.7
Nabis ferus		3.8		3		4.1

Table 20.--(cont.)

Reduviidae		1.9		1		14.7
Sinea diadema	2.0		1		13.3	
Lygaeidae		1.9		1		0.2
Coreidae						
Coreinae	2.0	1.9	1	1	7.5	14.9
Alydinae		1.9		2		14.3
Pentatomidae						
Thyanta sp.		5.7		4		34.4
Euschistus sp.	2.0	1.9	1	1	21.1	31.0
Cydnidae		3.8		11		8.0
Miscellaneous						
Immature		5.7		4		0.9
Adult		3.8		4		54.2
Homoptera						
Membracidae	12.2	7.5	8	5	23.8	14.4
Cicadellidae	6.1	1.9	7	2	9.1	3.1
Draeculacephala mollipes		5.7		5		17.9
Aphididae		9.4		60		9.6
Miscellaneous						
Immature	2.0	7.5	1	5	2.0	24.4
Adult		1.9		1		0.2
Coleoptera						
Carabidae	24.5	26.4	44	36	383.5	337.0
Hydrophilidae	2.0		2		17.6	
Elateridae	2.0	3.8	1	2	7.9	38.7
Coccinellidae						
Ceratomegilla fuscilabris		20.8		33		126.0
Cyclomeda sanguinea		3.8		2		5.4
Hippodamia convergens		35.8		62		357.9
Mycetophagidae		1.9		4		2.9
Scarabaeidae	2.0	1.9	1	1	8.4	17.7
Cerambycidae		1.9		1		18.5
Chrysomelidae	4.1	7.5	2	7	3.1	16.5
Cryptocephalinae		1.9		1		1.4
Galerucinae						
Diabrotica undecimpunctata		3.8		5		34.0
Eumolpinae		1.9		1		2.9
Chrysochus auratus	2.0		7		50.5	

Table 20.--(cont.)

Anthribidae		1.9		1		1.1
Curculionidae		11.3				[illegible]
Miscellaneous Larva	26.5	56.6	64	116	139.8	425.6
Pupa		11.3		10		30.0
Adult	8.2	3.8	4	3	15.3	48.7
Neuroptera Chrysopidae *Chrysopa* sp.		5.7		3		2.4
Lepidoptera Larva	69.4	67.9	105	111	1766.5	2358.0
Pupa	2.0	13.2	2	11	78.9	256.4
Adult	2.0	3.8	1	3	12.9	36.3
Diptera Sciaridae		1.9		1		0.4
Cecidomyiidae		3.8		40		6.8
Tabanidae	4.1		5		84.3	
Asilidae		1.9		1		48.2
Syrphidae		1.9		1		2.6
Piophilidae		1.9		35		46.2
Clusiidae		1.9		1		1.1
Anthomyiidae		3.8		2		3.2
Muscidae	2.0		1		0.8	

Table 20.--(cont.)

Tachinidae		5.7		5		63.6
Miscellaneous						
Pupa		1.9		1		2.6
Adult	2.0	1.9	1	1	0.3	0.7
Hymenoptera						
Mymaridae		1.9		1		+
Formicidae	4.1		2		18.1	
Myrmicinae	4.1	1.9	2	1	0.3	0.1
Formicinae						
Camponotus sp.	2.0	3.8	1	4	8.0	25.7
Miscellaneous						
Egg	2.0		1		0.2	
Larva		1.9		1		0.3
Pupa	4.1	3.8	2	2	8.2	16.3
Adult	12.2	11.3	6	7	12.3	59.4
PLANT KINGDOM						
Wheat Kernels	28.6	20.8	29	17	876.6	506.4
Mulberries		18.9		16		312.0
Miscellaneous Seeds	4.1	17.0	10	36	61.9	161.7
GRIT						
Snail Shells	2.0	15.1	1	16	2.9	30.0
Stones	10.2	18.9	7	16	76.6	67.8
TOTAL			364	781	4702.7	6102.1

Table 21.--Seasonal analysis of overlap in insect diets of nestling house sparrows and tree sparrows.

		Subsample Periods				
Species		5/14-6/1	6/2-6/15	6/16-6/28	6/29-7/17	7/18-8/14
House Sparrow	N	10	13	12	7	7
Tree Sparrow	N	8	12	20	7	6
$\hat{C}_\lambda$		0.9319	0.9993	0.9068	0.7810	0.5918

Table 22.--Utilization of nest-boxes at site B by house sparrows and tree sparrows subsequent to entrance hole enlargement of 21 nest-boxes in September 1971.

1972 Category[1]	N	House Sparrow	Tree Sparrow
1	9	8	1
2	6	0	6
3	21	10(13)[2]	11(8)[2]

1973 Category[1]	N	House Sparrow	Tree Sparrow
1	22	21	0
2	15	1	14
3	8	4	4

[1] Consult text for definitions of categories.

[2] Figures are for initial occupancy with final occupancy in parentheses (see text).

Table 23.--Number of young fledged per pair-season by the house sparrow and tree sparrow near Portage des Sioux, Missouri.

	House Sparrow S_1	Tree Sparrow S_2	S_1/S_2
# Clutches per Pair-season - A	2.40	2.61	1.09
Mean Clutch Size - B	4.64	4.99	1.08
Hatching Success - C	0.646	0.715	1.11
Fledging Success - D	0.628	0.724	1.15
Mean Number of Young Fledged per Pair-season - A x B x C x D	4.52	6.74	1.49

Table 24.--A comparison of hatching success and fledging success of the house sparrow at site B between low density years of the tree sparrow (1968-1970) and high density years (1971-1973).

	Date of Clutch Initiation				
	3/17-5/10	5/11-6/9	6/10-7/9	7/10-8/13	Total
Hatching Success					
1968-1970	63.1%	74.5%	70.7%	64.8%	68.6%
1971-1973	70.6%	65.0%	75.9%	57.8%	68.6%
Fledging Success					
1968-1970	74.0%	62.9%	74.1%	94.7%	73.8%
1971-1973	47.7%	65.1%	63.8%	87.1%	59.7%

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